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Diversidad y biogeografía de dinoflagelados marinos : notas en la taxonomía de algunos de los grupos menos conocidos

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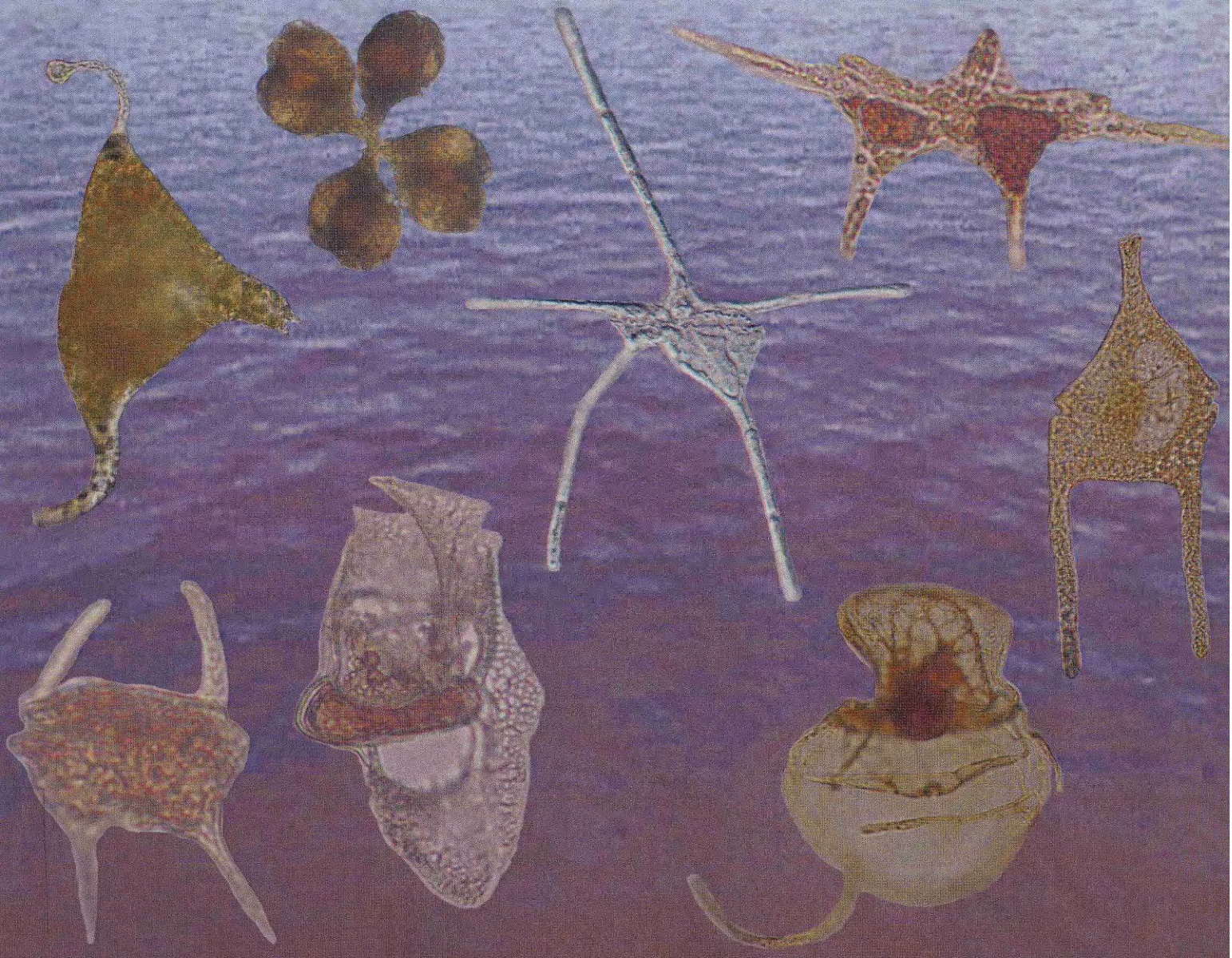

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"Una de las creaciones más prodigiosas de la Naturaleza, de las que más sublimes encantos encierran para el contemplador del Universo y más elevan el espíritu á las serenas y etéreas esferas del Infinito, es, sin duda, la de esos misteriosos seres diminutos, largos siglos ignorados de la humanidad, y aún hoy totalmente inadvertidos para la inmensa mayoría de las gentes que por motivos varios no auxilian su deficiente vista con el poderoso auxilio del microscopio"

Carús Falcón, 1903

A mi madre

Agradecimientos

Mi agradecimiento a Fidel Echevarría y Carlos M. García por darme la oportunidad de analizar mis primeras muestras de fitoplancton y a Manuel Varela por las primeras guías de identificación. Hervé Claustre me ha proporcionado muestras del Mediterráneo y del Pacífico Sur. En Japón, Ken Furuya me proporcionó excelentes muestras y me dio la mayor estabilidad laboral hasta ahora, 20 meses sin cambiar de laboratorio. De Yukio Nagahama aprendí técnicas de microscopía y Yasuwo Fukuyo compartió conmigo su bibliografía sobre dinoflagelados. De regreso a Europa, Sami Souissi me permitió continuar estudiando el fitoplancton.

Diez años tras de mi licenciatura, Blanca Pérez Uz me ha facilitado completar la tesis doctoral que tantas limitaciones me ha creado estos años.

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1. Introducción a los dinoflagelados

1.1 Historia de las investigaciones sobre dinoflagelados

1.1.1. Observaciones pre-microscópicas

Los dinoflagelados han sido conocidos desde siempre. Según algunas teorías los primeros homínidos comenzaron a consumir mariscos caracterizados por altos contenidos en ácidos grasos poli-insaturados y eso permitió el desarrollo del cerebro humano (Broadhurst *et al.*, 1998). Algunas especies de dinoflagelados producen toxinas que se acumulan en mariscos y peces. Así que estos primeros homínidos ya sufrieron las consecuencias de estos primeros contactos con los dinoflagelados. Las grandes proliferaciones de dinoflagelados, en su mayor parte asociadas con especies tóxicas, son capaces de producir coloraciones del agua. Este fenómeno, conocido comúnmente como mareas rojas, ha recibido multitud de nombres en la bibliografía científica como proliferaciones o floraciones algales nocivas (en inglés como *Harmful Algal Blooms* o su acrónimo "HAB") (Ochoa *et al.*, 2003).

Aunque es común referir como primer ejemplo de mareas rojas a la primera de las plagas que azotaron Egipto en tiempos de Moisés cuando "las aguas del Nilo se transformaron en sangre..." (Éxodo 7: 19-21; 1491 a.C.), ese ejemplo es muy dudoso que estuviese asociado con dinoflagelados porque las mareas rojas de dinoflagelados son poco frecuentes en aguas fluviales. Años más tarde, los israelitas añadieron el marisco en su lista de alimentos prohibidos, alejándoles de los problemas causados por los dinoflagelados (Deuteronomio 14: 9-10, ~1451 a.C.). Los antiguos griegos atribuían las mareas rojas a la furia de Neptuno. En la Edad Media se hablaba de la 'purga de mar' como una purificación de los fondos marinos y muchas otras teorías aparecieron hasta finales del siglo XIX (Sobrino, 1918; Kofoid y Swezy, 1921). En la sabiduría popular aparecían reglas como evitar comer mariscos en los meses que no tuvieran la letra "r", es decir entre mayo y agosto, cuando los dinoflagelados suelen alcanzar sus mayores abundancias. No es posible diferenciar a simple vista el marisco contaminado, así que las intoxicaciones han continuado, sobre todo en islas tropicales donde el marisco es casi la única fuente de proteínas.

Además de las mareas rojas, otro fenómeno visible asociado con los dinoflagelados es la bioluminiscencia. Las primeras referencias conocidas

aparecen en el Mediterráneo (Anixímenes, 500 a.C.; Aristóteles, 350 a.C.; Titus Livius, 215 a.C.; revisado en Harvey, 1957). En las noches más oscuras durante el verano se veían pequeños destellos luminosos en los rompeolas y las estelas de los barcos dejaban un rastro de luz tenue. Este fenómeno es más llamativo en aguas tropicales como en la Bahía Fosforescente de Puerto Rico o el *Fire Lake* en Bahamas, pero la presión turística terminó por alterar las comunidades de dinoflagelados. En el 77 a.C. el naturalista griego Plinio describe 'fuegos que aparecen repentinamente en las aguas'. La palabra griega "pyrrhos" (=fuego, llama) sería dos milenios más tarde usada para nombrar a los dinoflagelados como Pyrrhophyta (Pascher, 1914). En la novela *'20.000 leguas de viaje submarino'* escrita por Julio Verne en 1869, el capitán Nemo a bordo del *'Nautilus'* describió en su paso por el Índico: *"Era un 'mar de leche', una balsa de agua que brillaba en la oscuridad...debida a la presencia de miríadas de infusorios"*. Recientemente se publicó por primera vez una imagen de satélite de un *'milky sea'* con más de 250 Km. de longitud (Miller *et al.*, 2005). En este caso se trataba de bioluminiscencia y no del color blanco asociado con la proliferación de algunos cocolitofóridos. A menor escala la bioluminiscencia es un fenómeno común en mares tropicales, especialmente en el Océano Indico, Golfo Pérsico y el Mar del Sur de la China. Los marinos describen como unos 'discos' o 'ruedas' brillantes se desplazan a ras de las aguas (Herring y Horsman, 1985). En el Océano Pacífico *Lingulodinium* (=*Gonyaulax*) *polyedra* tiende a agruparse y migrar verticalmente formando círculos luminosos de centenares de metros de diámetro. No han faltado interpretaciones sobre el origen de estas luces como bases submarinas de OVNIs (Ribera, 1966).

Desde un punto de vista ecológico, la bioluminiscencia en dinoflagelados se ha interpretado como un mecanismo que les permite reducir la presión de sus depredadores. En la noche cuando el dinoflagelado detecta vibraciones de un posible depredador que se acerca, generalmente un copépodo, produce un destello que llama la atención de un segundo depredador. Pequeños peces se acercan a la fuente de luz que esta delatando la presencia de un copépodo para depredarlo. Los copépodos 'saben' que ese destello revela su posición ante sus depredadores y se alejan rápidamente sin atacar al dinoflagelado. El minúsculo dinoflagelado bioluminiscente no es de interés para los peces y ha eliminado a su depredador directo (Buskey y Swift, 1983).

Los dinoflagelados son responsables de barreras de coral de miles de kilómetros observables incluso desde el espacio. En un contexto de incremento de niveles de dióxido de carbono, las zooxantelas, unos dinoflagelados simbióticos en invertebrados marinos (esponjas, anémonas, gasterópodos, turbelarios, etc.) y especialmente en pólipos (*Symbiodinium* spp.) son de una extrema importancia en el ciclo del carbono a través de la formación de los arrecifes de coral (Marshall, 1996).

1.1.2. Primeras observaciones microscópicas[1]

Aunque las grandes concentraciones de dinoflagelados puedan ser visibles al ojo humano, individualmente las células al ser menores de 1 milímetro, no son visibles a simple vista. Algunas especies bioluminiscentes como *Noctiluca*, *Pyrocystis* o *Leptodiscus* alcanzan diámetros de hasta dos milímetros, siendo visibles al ojo humano, aunque no lo suficiente como para distinguir su morfología.

Desde antiguo, el pulido de cristales permitía fabricar rudimentarias lentes que apenas alcanzaban una magnificación de 10 aumentos. A finales del siglo XVI comienzan a fabricarse lentes de mayor calidad, principalmente por artesanos holandeses como Z. Janssen (~1588-~1632) o J. Lipperhey (1579-1619) que en aquel tiempo eran simplemente usadas en espectáculos. Galileo Galilei (1564-1642) conoció de la existencia de esas lentes y en 1609 las utilizó en un rudimentario 'Occhiolino', combinando una lente cóncava y convexa para observar los ojos de una mosca. Francesco Fontana (1580-1656) en Nápoles usaría las primeras lentes convergentes en 1618. En 1619, el holandés Cornelius Drebbel (1572-1633) presentó uno de estos primeros microscopios en Londres y en 1625 Johannes Faber (1574-1629) establece el término microscopio (derivado del griego: *micros*=pequeño y *skopien*=ver, observar). El filósofo italiano Petrus Borellus remarcaba que el microscopio sería útil para investigar los misterios de la naturaleza. En 1665, Robert Hooke (1635-1703) con un microscopio de 30 aumentos describió unas 'celdillas' en el corcho en su *Micrographia Illustrata*. Dos siglos después esas 'celdillas' recibirían el nombre de células. Antony van Leeuwenhoek (1632-1723) fabricó un microscopio que podía alcanzar hasta 270 aumentos y ayudado de una supuesta prodigiosa agudeza visual describe entre

[1] Una revisión histórica de la descripción de los primeros dinoflagelados puede encontrarse en Kofoid y Swezy (1921), Taylor (1980a) y Taylor (1987). Mi gratitud a M.O. Soyer-Gobillard (CNRS, Banyuls), M. Sandrine (Biblioteca, Banyuls) y P. Assmy (AWI-Bremerhaven) por la bibliografía y datos biográficos de autores.

1674-1716 sus observaciones de animálculos, traducidas como "*living atoms*" o "*little animals*" en sus cartas a la *Royal Society* de Londres. Sus cartas constituyen la primera descripción de protistas. Van Leeuwenhoek incluiría las primeras descripciones de frústulas de diatomeas en 1702, sin aparentemente ningún dinoflagelado.

Entre las especies de dinoflagelados más accesibles estaría *Noctiluca*, que por su gran tamaño y bioluminiscencia llamaba la atención a esos primeros observadores en las costas europeas y la especie epicontinental *Ceratium hirundinella*, muy común en los embalses europeos. No esta claro quien fue el primer observador de *Noctiluca* con un microscopio. El yerno de Daniel Defoe, Henry Baker (1698-1774), incluyó un capítulo titulado "Of luminous water insects" en su libro *Employment for the Microscope* publicado en 1753. Baker cita una carta donde Joseph Sparshall describe que observó un animálculo de las costas de Norfolk (Mar del Norte) que emitía luz al ser agitado. Sparshall observó el 'insecto luminoso' con un microscopio y preparó una ilustración para el libro de Baker, pero que al parecer no llego a tiempo a la imprenta (según Harvey, 1957). Fueron muchos otros los observadores de la bioluminiscencia de *Noctiluca* en las costas atlánticas europeas, por ejemplo J.B. Leroy en 1754, J. Baster en 1957, P. Forsskål en 1762 o M. Rigaut en 1765, pero sin ilustrarla. La primera ilustración de *Noctiluca* a partir de una observación microscópica aparecería en el libro de Martinus Slabber (1740-1835) publicado en 18 partes entre 1769 y 1778. Este holandés aficionado a la zoología, publica en 1771 su plancha VIII, dibujada por P.M. Brasser y él mismo (Fig. 1), donde ilustra una *Noctiluca*.

Fig. 1. *Noctiluca*, primer dinoflagelado ilustrado (Slabber, 1771).

Algunos observadores de la época como Louis Joblot (1645-1723) en 1718 ilustraban a los infusorios con formas monstruosas o satíricas y eso restaba credibilidad a la existencia de esos organismos. A partir de 1753 en botánica y 1758 en zoología se comenzó a utilizar la nomenclatura binomial propuesta por Carl von Linneus (1707-1778). Linneo, un botánico con poca confianza en las posibilidades del microscopio, no incluyó ninguno de los que él llamaba 'animales invisibles' hasta la edición X del *Systema Naturae* en 1758, incluyéndolos en la

clase Vermes y en su último orden, con el ambiguo nombre de Zoophyta. En la edición XII en 1767, los pocos géneros de protistas que Linneo incluyó recibían nombres como *Chaos*, reflejando su desconfianza hacia esos 'animales invisibles' que se empezaban a describir.

En 1753, Martin Ledermüller introduce el término 'animales de infusiones' para todos estos pequeños organismos que aparecían en infusiones. El término sería latinizado como *Infusoria* por H.A. Wrisberg en 1763. En 1818 aparecería el término Protozoa utilizado por primera vez por Goldfuss (1818) y aparecerían con carácter de reino: Protozoa por Owen (1859), Regnum Primigenum (Protoctista) por Hogg (1860) y Protista por Haeckel (1866) (revisado por Rothschild, 1989).

En 1762 P. Forsskål (1732-1763) había usado 'medusa noctiluca' para referirse a *Noctiluca.* Slabber en 1771 usa el nombre de 'medusa marina'. '*Noctiluca*' ya existía para designar a otros organismos con capacidad de brillar en la oscuridad y un anélido marino, actualmente *Nereis*, había recibido el nombre de '*Noctiluca marina*' en el *Systema Naturae* de Linneo (1758). El primer nombre genérico de un dinoflagelado pudo ser *Gleba*, propuesto para *Noctiluca* en 1791 por J.G. Bruguière (1749-1798). Según Bütschli (1880-1882, p. 1031) Bruguière había reproducido las figuras de Slabber (1771). Sin embargo, ya por aquel entonces el género *Gleba* estaba previamente ocupado y era un homónimo posterior de moluscos descritos póstumamente en 1776 por Forsskål. El género *Gleba* de Bruguière no era binomial y nunca estuvo en uso. Al igual que Slabber (1771), Macartney observó *Noctiluca* en el Mar de Norte y en 1810 propuso el nombre *Medusa scintillans*. En 1815, L. Oken (1779-1851), se refiere a *Noctiluca* como *Slabberia*, dedicando el género a M. Slabber, pero sin utilizar la nomenclatura binominal. En 1816, Lamarck (1744-1828) crea el epíteto *miliaris* y utiliza *Noctiluca* como género inspirándose en 'Noctiluque' que aparecía en un manuscrito de M. Suriray (1769-1846). En 1836, Suriray describe formalmente *Noctiluca miliaris*, a partir de una comunicación fechada en 1810. Ehrenberg (1834) en su 'Das Leuchten des Meeres' propone *Mammaria scintillans* para referirse a *Noctiluca*. El nombre *Mammaria* ya aparecía listado por O.F. Müller en 1776/1777 y quedó en desuso. Otros epítetos aparecerían para describir a *Noctiluca*, considerando que se trataba de diferentes especies en cada océano. Busch (1851) propone *Noctiluca puntata* y Giglioli (1870) *Noctiluca omogenea* y *N. pacifica*. En la actualidad se acepta una sola especie como *Noctiluca scintillans*

(Macartney 1810) Kofoid 1920 (Sournia, 1984). *Noctiluca scintillans* presenta pequeñas variaciones geográficas. Así por ejemplo *N. scintillans* no presenta bioluminiscencia en el Pacífico norte y sólo en el sudeste asiático prolifera la '*green Noctiluca*' que presenta unos flagelados endosimbiontes que nadan libremente dentro de la célula (Finlayson, 1826). *Noctiluca* no presenta la morfología típica de un dinoflagelado y se mantuvo alejado de los dinoflagelados en el grupo Cystoflagellata desde Haeckel (1873) hasta Kofoid (1920). Hoy en día aún no está clara su posición filogenética debido a la falta de información de secuencias de ADN de otras Noctilucales.

El primer dinoflagelado con las características típicas de este grupo fue publicado por el danés Otto Friedrich Müller (1730-1784) y descrito siguiendo las reglas de Linneo en su obra póstuma *Animalcula Infusoria* junto con otras 300 especies de infusorios que él consideraba como un tipo de gusanos (O.F. Müller, 1786). Entre sus infusorios se encontraban los dinoflagelados epicontinentales: *Bursaria* (*Ceratium*) *hirundinella* y *Vorticella* (*Peridinium*) *cincta*, cuyas diagnosis ya se publicaron en 1773 y *Cercaria* (*Ceratium*) *tripos*, una especie marina listada en 1776/1777 (ilustrada en 1781, p. 206). O.F. Müller no ilustró ningún flagelo, pero describe una fila de pequeños cilios alrededor de la célula en su observación del movimiento de *Cercaria* (*Ceratium*) *tripos*: "*Motus lentus ope forte ciliorum fubtus conditorum*". Las denominaciones *Bursaria* y *Vorticella* son actualmente géneros de ciliados y *Cercaria* no fue incluida en los trabajos posteriores de Ehrenberg, siendo un término usado para las larvas acuáticas de tremátodos.

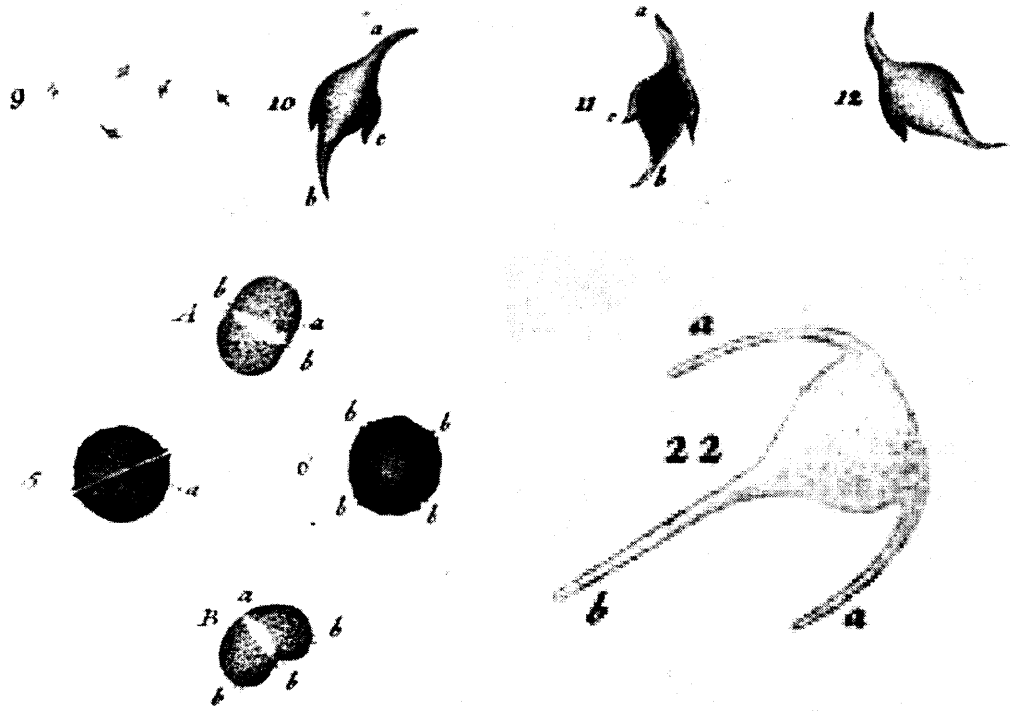


Fig. 2. Ilustraciones de los primeros dinoflagelados descritos tras *Noctiluca* por O.F. Müller (1786).

En 1793, Franz Paula von Schrank (1747-1835) describe *Ceratium pleuroceras* y *C. tetraceras*, siendo el primer género de dinoflagelados aún vigente. En 1802 también describe *Ceratium macroceras*. Esas especies son sinónimas de *Ceratium* (*Bursaria*) *hirundinella*, muy común en los embalses europeos y previamente descrito por O.F. Müller.

En 1830, Gustav Adolph Michaelis (1798-1848) demostraba que los infusorios podían producir bioluminiscencia en las aguas del puerto de Kiel. Además del ya conocido *Cercaria* (*Ceratium*) *tripos*, Michaelis ilustra bajo el nombre de *Cercaria* sp. y *Ceratium* sp., las especies que poco después serían *Prorocentrum micans* Ehrenberg 1834, *Peridinium* (=*Ceratium*) *fusus* Ehrenberg 1834 y un '*Volvox*', un *Protoperidinium* que podría corresponder a *Peridinium divergens* Ehrenberg 1841 y que recibiría el nombre *Peridinium michaelis* Ehrenberg 1840/1841. Después otro *Peridinium michaelis* Stein 1883 aparecía, quizás en referencia a especimenes que aparecen en la parte central de su plancha y que podrían corresponder a *Peridinium steinii* Jørgensen 1899. Michaelis ilustraba sus especimenes de *Ceratium tripos* con tres flagelos (Fig. 3). El 'filamento motor' vibraba barriendo un área cónica y Michaelis lo interpretó como si hubiese varios flagelos posteriores. Esta fue la primera ilustración de un flagelo en dinoflagelados.

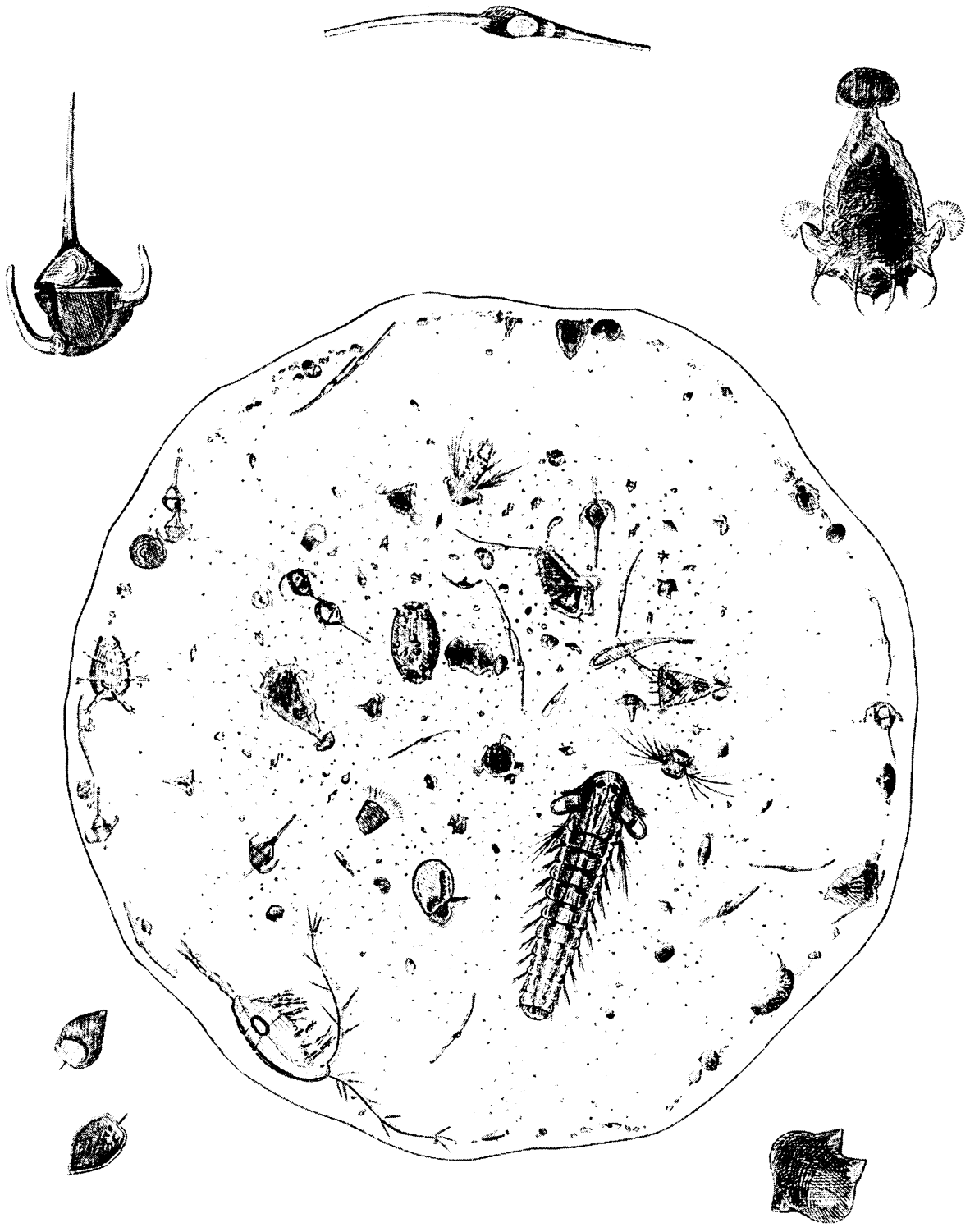


Fig. 3. Plancha publicada por Michaelis (1830) donde se ilustran por primera vez el flagelo de los dinoflagelados, aunque erróneamente, como 3 flagelos longitudinales. También aparecen por primera vez los géneros *Protoperidinium* y *Prorocentrum* y la especie *Ceratium fusus*.

Christian Gottfried Ehrenberg (1795-1876) en torno a 1830/1832 erigió los géneros *Peridinium* y *Glenodinium*, agrupándolos en la familia Peridinaea. También describió el dinoflagelado epicontinental *Peridinium fuscum* que después sería la especie tipo del género *Gymnodinium* en Stein (1878, p. 89) y el género *Dinophysis* en 1834/1840. Sin embargo, Ehrenberg no relacionó a *Dinophysis*, con los dinoflagelados que había descrito. Las fechas de las descripciones de sus especies varían en la bibliografía: unas veces se cita la fecha de presentaciones orales, otras la publicación de la diagnosis y otras la publicación de las ilustraciones. En estos primeros nombres de dinoflagelados aparecía el término griego 'dino, dinium' (=rotación, giro) que hacía referencia al característico movimiento de los dinoflagelados rotando sobre su eje longitudinal y desplazándose en una trayectoria helicoidal. Nada tiene que ver con 'dino' en dinosaurio que viene del griego 'din-o' o 'dein-o' (=terrible, monstruoso). En Sorrento, Ehrenberg describió *Prorocentrum lima* como *Cryptomonas lima* dentro del grupo de las criptofíceas. Ehrenberg (1838/1840) observó microfósiles y en su 'xanthidia' estaba describiendo un *Peridinium* fósil. A partir de fósiles también describe el género *Actiniscus*, que Schütt en 1891 encontraría vivo en el plancton. En 1850, el geólogo Mantell (1790-1852) había descrito ilustrado *Spiniferites*, hoy en día reconocido como la forma fósil de *Gonyaulax*.

Estudios previos revelaban que estos organismos microscópicos eran más simples en su organización que los animales superiores. Sin embargo a Ehrenberg le sorprendió la complejidad de los infusorios y presentó su monografía *Die Infusoriensthierchen als vollkommene Organismen* antes de que Schwann y Schleiden formulasen la teoría celular por separado en 1838-1839. Con este título de 'Los *pequeños animales* infusorios como organismos completos', Ehrenberg consideraba a los infusorios como animales en miniatura. Así por ejemplo, los cromatóforos eran ovarios, el núcleo era la próstata y las vacuolas eran estómagos. A pesar de disponer de un buen microscopio, no parecía tener confianza en lo que observaba con grandes magnificaciones y sus estudios se limitaban a un máximo de 300 aumentos. Al no observar detalles internos de la célula, Ehrenberg continuó con la idea intuitiva de animales en miniatura, lo que obstaculizaba que aceptara las teorías evolutivas que en 1859 Charles Darwin (1809-1882) presentó en *The origin of species by means of natural selection*.

Félix Dujardin (1801-1860) en 1834 fue el primero en rebelarse contra esta idea de 'pequeños animales' al demostrar que el citoplasma de los foraminíferos no era pluricelular. Dujardin divide a esos 'animales unicelulares' en función de su tipo de locomoción, *Infusoria* para especies provistas de flagelos o cilios y *Rhizopoda* para los que se desplazaban por otro medio, por ejemplo con pseudópodos. Sin embargo la influencia de Ehrenberg era tan grande que sus ideas se mantendrían varias décadas más, lo que no contribuyó al avance de la protistología con independencia de la zoología (Sokin, 2001). Por ejemplo todavía en 1891, J. Pelletan consideraba a las diatomeas como organismos pluricelulares. Dujardin (1841) describe *Oxyrrhis marina*, que es ahora considerado un dinoflagelado primitivo (Gao y Li, 1986). Dujardin al igual que Ehrenberg seguía viendo una fila de pequeños cilios alrededor del cíngulo de los dinoflagelados (Fig. 4).

Fig. 4. *Ceratium tripos* con una fila de cilios en el cíngulo según Dujardin (1841).

En 1845, Johannes Müller (1801-1858) introducía en Helgoland a sus estudiantes como Ernst Haeckel (1834-1919) en el estudio de los organismos microscópicos pelágicos. J. Müller fabricó una finísima malla que recogía lo que él denominaba '*Auftrieb*'. En 1855 entre sus descripciones de radiolarios incluyó a *Thalassicolla*, que podría estar cercano a *Physematium atlanticum* Meyen (1834). En Messina y Niza, J. Müller había observado un infusorio bioluminiscente en sus muestras de zooplancton, con el aspecto de una *Noctiluca* sin apéndice y que se consideraba la forma enquistada de *Noctiluca*, pero en realidad debía ser *Pyrocystis*. Por aquel entonces, la bioluminiscencia que llamaba la atención a los navegantes en aguas abiertas de mares tropicales se atribuía a *Noctiluca*. Sin embargo, en la mayor parte de los casos se debía a *Pyrocystis*, ya que *Noctiluca* suele ser más común en las zonas costeras más eutróficas. Quizás las primeras descripciones de *Pyrocystis* fueron las especies *Mammaria adspersa* von Tilesius (1814) o *Physematium atlanticum* Meyen (1834), pero las ilustraciones no son suficientemente detalladas. Estos infusorios bioluminiscentes o

'*Infusionsthierchen*' en mares cálidos (Gilbert, 1819; Baird, 1830) muy probablemente se trataban de *Pyrocystis pseudonoctiluca.* A partir de observaciones durante la expedición científica del *Challenger* (1873-76) que había circunnavegado el globo, John Murray en C. Wyville Thomson (1876) describía *Pyrocystis pseudonoctiluca* y *P. fusiformis*, aunque inicialmente como diatomeas. En 1885, Murray incluiría las ilustraciones y discutía sobre la posición sistemática de *Pyrocystis* como un infusorio. Según Murray (1885), los rudimentarios análisis químicos mostraban la existencia de sílice. La pared de dinosporina que caracteriza a los quistes vegetativos de *Pyrocystis* era el origen de la confusión sobre su sistemática. En 1890, Haeckel incluiría el género *Pyrocystis* citado por J. Murray como un dinoflagelado y en 1891 lo redescribiría como *Murracystis*. Años más tarde, la observación de estados de vida con células que se asemejaban a *Gonyaulax* en el interior de los quistes de *Pyrocystis* llevó a Kofoid y Swezy (1921) a relacionarlo con ese grupo de dinoflagelados, confirmado recientemente mediante biología molecular.

En 1859 dos discípulos de J. Müller, Édouard Claparède (1832-1871) y Johannes Lachmann (1832-1860), publicaron sus observaciones de protistas en Bergen. Describieron el género *Amphidinium*, establecieron *Prorocentrum* como un dinoflagelado y llamaron la atención sobre la formación de quistes en dinoflagelados. Claparède y Lachmann (1858-61) dividieron a los infusorios en cuatro órdenes e incluyeron los dinoflagelados en Cilioflagellata. Aún se interpretaba el flagelo transversal como una fila de cilios y los dinoflagelados eran por tanto intermedios entre los ciliados y los flagelados. Los términos Ciliata y Flagellata habían aparecido recientemente con Perty y Cohn en 1852 y 1853, respectivamente.

Los avances fueron escasos durante las dos décadas siguientes. Ehrenberg y sus ideas de animales en miniatura seguían teniendo una gran influencia. Los dinoflagelados se consideraban estadios embrionarios de anélidos Nereidos y eso influyó por ejemplo en la descripción de género *Gonyaulax* como una larva de un anélido (Diesing, 1866). *Polykrikos*, con varios núcleos y varios pares de flagelos, fue inicialmente considerado como la larva de un turbelario pelágico, en 1873 como un ciliado por Bütschli y en 1881 Bergh lo asociaría con los dinoflagelados. En 1875 J. Warming (1841-1924) demostró que la teca de los dinoflagelados estaba compuesta de celulosa. Warming consideró a los dinoflagelados como plantas, intermedios entre las diatomeas y las desmidiaceas.

Otro factor que no contribuía al avance de los estudios de dinoflagelados era la falta de microscopios. A partir de 1847 Carl Zeiss (1816-1888) comienza a fabricar microscopios en Jena, perfeccionándolos con la asistencia de E. Abbe (1840-1905) y O. Schott (1851-1935). En 1866, Zeiss había vendido 1000 microscopios que empezaban a llegar a los microbiólogos de la época. En 1868, Filippo Pacini (1812-1883), descubridor de agente causante del cólera, diseñó y mando construir un microscopio invertido, que ya eran utilizados para observar reacciones químicas.

Brandt (1881) describe las zooxantelas (*Zooxanthella* spp. / *Symbiodinium* spp.) como protistas simbiontes en radiolarios coloniales y pólipos. Bergh (1881) describió *Diplopsalis*, *Protoceratium* y *Protoperidinium* y dividió el orden Cilioflagellata en dos familias, la Adinida que incluía *Prorocentrum*, y la Dinifera. Esta última la dividió en subfamilias, Dinophyida, con *Dinophysis* y *Amphidinium*, Peridinida, para *Peridinium* y especies relacionadas, Gymnodinida para *Gymnodinium*, *Hemidinium* y *Polykrikos*. *Amphidinium* permaneció aún por algunos años lejos de *Gymnodinium* en las clasificaciones.

1.1.3. De Cilioflagellata a Dinoflagellata

El año 1883 fue clave debido a los trabajos de Friedrich Ritter von Stein (1818-1885), Georges Pouchet (1833-1894), Georg Klebs (1857-1913) y Paul Gourret (1859-1903). El gran impulso a la diversidad de dinoflagelados marinos se debió a Stein que escribe la primera monografía sobre dinoflagelados (1878, 1883) (Fig. 5).

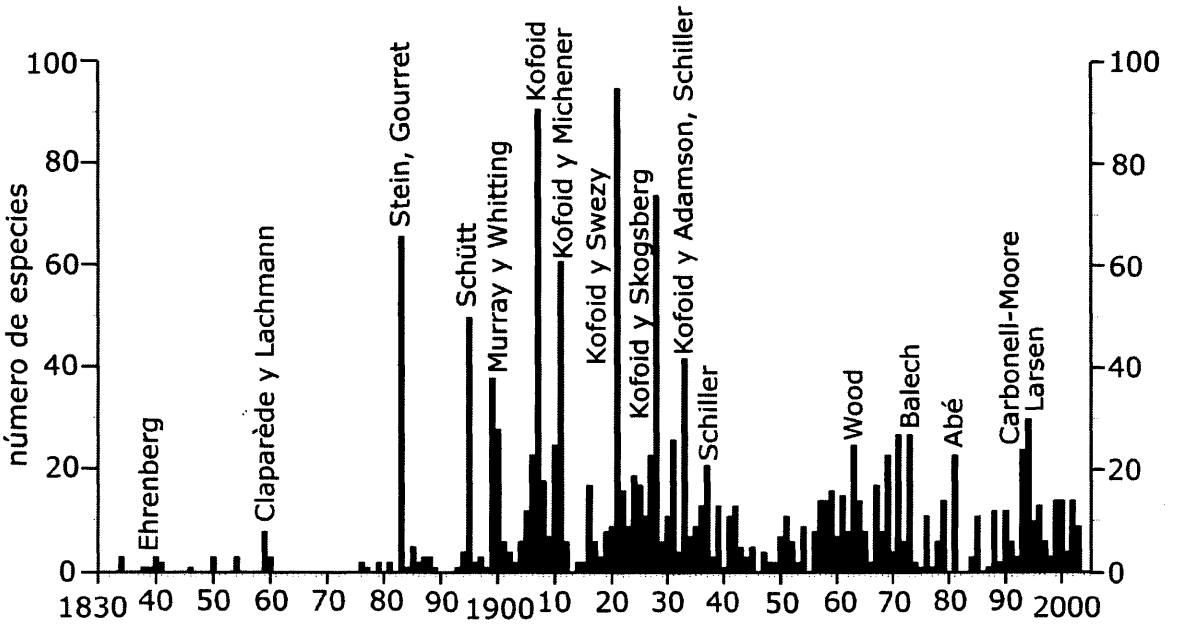


Fig. 5. Evolución histórica en la descripción de especies de dinoflagelados basado en Gómez (2005).

Hasta entonces las especies marinas investigadas debían ser muy abundantes y fácilmente accesibles en las costas europeas. Exceptuando *Pyrocystis*, la diversidad de dinoflagelados en aguas tropicales era desconocida. Estudiar muestras oceánicas requería fijarlas antes del análisis en el laboratorio. Cada investigador probaba diferentes sustancias como fijadores, generalmente con bebidas alcohólicas. En 1829, J. Lugol comenzó a utilizar soluciones de iodo y se extendió su uso como fijador y en tinciones. Otros autores utilizaban el ácido ósmico, más común entre los histólogos. El formol sintetizado por A. Butlerov en 1859 tardaría aún en popularizarse como fijador.

La baja abundancia de dinoflagelados en aguas abiertas de mares tropicales requería una técnica de concentración además de la fijación. Las mallas de plancton con un tamaño de poro pequeño eran difíciles de construir y otros métodos, como la técnica Utermöhl que combinaba la concentración por sedimentación con la microscopía invertida tardaría algunos años en aparecer. Los estudios de diatomeas avanzaban más rápidamente porque las frústulas se conservaban mejor y por ejemplo en unos gramos de guano podían encontrarse millones de frústulas de especies tropicales. Stein usa un método ingenioso de concentración al examinar los contenidos digestivos de las medusas y salpas del Mediterráneo y Polinesia y describe numerosos géneros, incluyendo casi todos los géneros de Dinophysiales (Fig. 6).

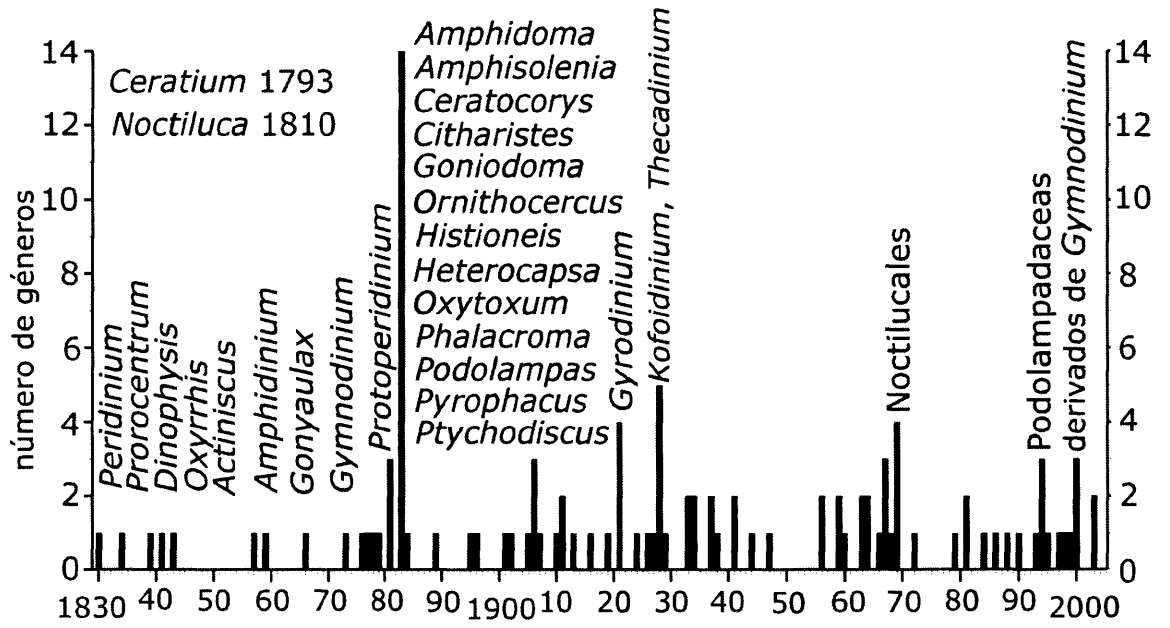


Fig. 6. Evolución histórica en la descripción de géneros de dinoflagelados basado en Gómez (2005).

Stein establece las bases de la tabulación en dinoflagelados tecados al reconocer las placas tecales en series latitudinales: Frontalia (placas apicales), Basalia (placas precingulares) y Mundspalta (pequeñas placas alrededor de los poros de los flagelos). Paul Gourret ese mismo año había publicado un completo estudio de los dinoflagelados del Golfo de Marsella. La monografía de Stein fue publicada en noviembre de 1883, pero no se conoce la fecha exacta del trabajo de Gourret. El género *Parrocelia* en Gourret perdió la prioridad frente a *Podolampas* en Stein. En cualquier caso, aún demostrándose que el trabajo de Gourret es anterior, *Podolampas* continuaría como *nomen conservatum.* En Stein y Gourret, al igual que muchos estudios previos, las ilustraciones no iban acompañadas de escala o información sobre la magnificación, ocasionando algunos problemas por posteriores interpretaciones erróneas del tamaño.

En 1859 Félix-Archimède Pouchet publicó *Hétérogénie, ou Traité de la génération spontanée* defendiendo la tradición creacionista en contra de Louis Pasteur. En ese mismo año se creó en Concarneau (Bretaña) la primera Estación de Biología Marina del mundo donde su director, hijo de Félix-Archimède, Georges Pouchet disponía de material abundante y observó los dinoflagelados aplicando una técnica de fijación con osmio. Klebs (1883) y Pouchet (1885) destacan el peculiar núcleo de los dinoflagelados. Ambos autores ilustraban los

dinoflagelados con el hiposoma en la parte superior. Stein (1883) consideraba que el flagelo longitudinal daba tracción en la parte posterior de la célula, contrariamente a interpretaciones previas, aunque aún ilustró algunas de las especies con el hiposoma en la parte superior.

A pesar de estos avances, aún continuaba vigente la idea de una fila de cilios que rodeaba al cíngulo de los dinoflagelados. Se habían observado los dos poros flagelares en dinoflagelados, pero interpretándolos como diferentes orígenes de un solo flagelo. Gourret (1883, p. 18-19) escribía "*Ces deux origines du flagellum sont aussi communes l'une que l'autre, mais constantes pour une même espèce*" e insistía "*Le flagellum enfin est toujours unique. Je rappellerai seulement que chez le* Cerat. cornutum, *Claparède a vu deux flagellum, dont l'existence constante est mise en doute même par ce naturaliste*". Pouchet (1883, p. 418) publicó "*Le fond du sillon vibratile paraît formé chez d'autres genres voisins (Peridinium, Protoperidinium, etc...) d'une piece unique rubanée – percée de deux rangs de pores, au dire de Bergh, par lesquels passeiraient deux rangées de cils vibratiles. On a vu que l'existence de ces pores nous semblait fort douteuse*". Como se asumía que los dinoflagelados tenían cilios en el cíngulo, había autores como Bergh que veían los poros por donde salían los cilios. Pouchet (1883, p. 429) en su descripción de *Amphidinium* escribía: "*mais nous ne saurions actuellement décider si celui-ici est dû à une couronne de cils ou a un second flagellum*". Pouchet (1883) no dibujaba nada en el cíngulo de los dinoflagelados. Stein (1883) ilustraba un flagelo ondulado desprendido del cíngulo como otros autores de la época (Fig. 7), pero no lo asociaba con el flagelo transversal y seguía representando una fila de cilios en el cíngulo.

Por aquellos años, *Polykrikos*, una célula pseudocolonial con múltiples cíngulos y flagelos, ofrecía una oportunidad de observar la verdadera naturaleza del flagelo transversal, pero también constituía un problema porque su aspecto general servía de argumento para relacionar a los dinoflagelados con los ciliados. Bergh (1881) había descrito *Polykrikos auricularia* (sinónimo de *Polykrikos schwartzii* Bütschli 1873) y aún ilustró una fila de cilios en sus cíngulos. Gourret (1883) sugería que *Polykrikos* no era más que células fusionadas de *Gymnodinium*, pero para Klebs *Polykrikos auricularia* era un verdadero ciliado. Tampoco Klebs estaba acertado cuando negaba que los dinoflagelados pudiesen ingerir otras células como Stein y Bergh habían observado en especies marinas como *Gymnodinium/Gyrodinium*. Esta consideración parecía común entre los

investigadores de especies epicontinentales como Klebs, probablemente porque las especies de agua dulce son generalmente autótrofas, mientras que las especies heterótrofas son más comunes en aguas marinas. Quizás por esa razón, Warming había propuesto a los dinoflagelados como intermedios entre diatomeas y desmidiaceas.

Klebs (1883) estuvo más acertado en sus observaciones de los flagelos. Por más que miraba en *Glenodinium cinctum* y *Peridinium tabulatum*, Klebs no observaba una fila de cilios en el cíngulo como afirmaban todos sus antecesores. Además del flagelo longitudinal, en *P. tabulatum* sólo observaba un segundo flagelo ondulante *"ein schraubig gewundenes Band"* y en principio consideró que esta característica era sólo de las especies de agua dulce. Klebs a menudo veía como sus colegas representaban a la especie marina *Ceratium tripos* con uno o dos flagelos posteriores. El flagelo longitudinal carece de mastigonemas, es liso, más fino y desaparece rápidamente al fijar o al manipular a la célula viva para su observación. El flagelo transversal es ondulado, más grueso al tener mastigonemas y más resistente. En muchos casos se estaba representando al flagelo transversal desprendido del cíngulo, considerando como el flagelo posterior (Fig. 7).

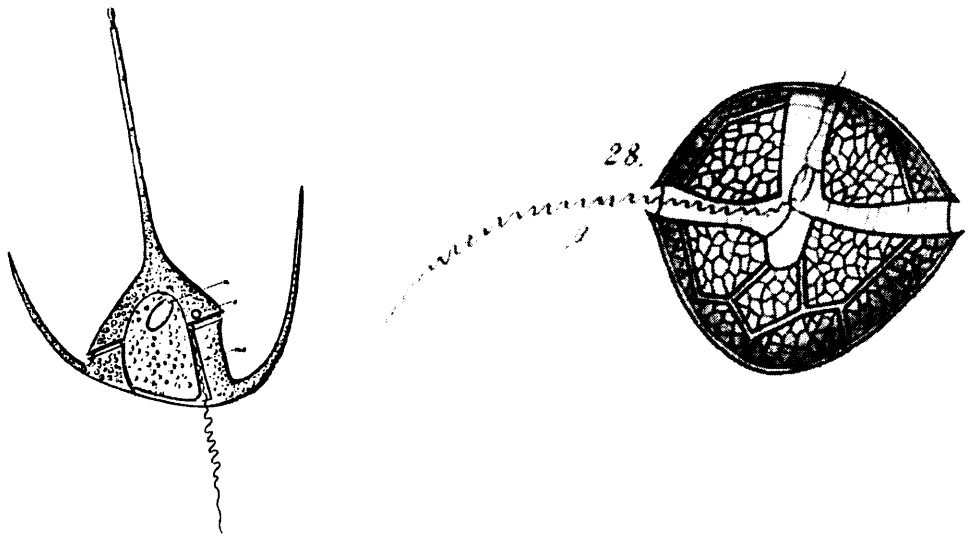


Fig. 7. Ilustración de *Ceratium tripos* con un flagelo ondulante en Stein (noviembre de 1883). Klebs (1883) por primera vez considera que el flagelo transversal es ondulante y no existe una fila de cilios en el cíngulo.

Klebs consideró que el flagelo ondulante se había desprendido del cíngulo y por tanto que también las especies marinas de dinoflagelados tenían un flagelo ondulante en el cíngulo y no una fila de cilios. Klebs (1883) daría el paso definitivo al ilustrar en *Peridinium tabulatum* ambos, un flagelo transversal ondulado y un flagelo longitudinal liso (Fig. 7). Es difícil entender cómo se necesitó un siglo para corregir la interpretación de O.F. Müller. Sólo puede explicarse por la influencia que aún el *opus magnus* de Ehrenberg tenía y que cada observador dudara antes de ir en contra de todas las interpretaciones previas.

El número de especies había crecido enormemente en 1883 (Fig. 5), los dinoflagelados no tenían cilios y necesitaban un nombre para reemplazar el término Cilioflagellata. En 1885, Otto Bütschli (1848-1920) propone Dinoflagellata al establecer el orden Dinoflagellida en la terminología zoológica y después aparecería Dinophyta o la clase Dinophyceae para los botánicos (West y Fritsch, 1927).

A finales del siglo XIX la distinción entre dinoflagelados tecados y atecados aún no se había realizado y *Amphidinium* continuaba agrupado con *Dinophysis*. Gourret (1883) consideraba que *Gymnodinium* derivaba de *Glenodinium* y *Diplopsalis* y que *Amphidinium* derivaba de *Dinophysis*. En 1895, Franz Schütt (1859-1922) describe numerosas especies de dinoflagelados atecados de aguas oceánicas. Schütt no menciona la localización geográfica de sus especies, lo que en la actualidad dificulta el estudio de la especie tipo. Un año después, Schütt revisa la clasificación de los dinoflagelados y por primera vez aparece la separación entre dinoflagelados atecados y tecados (Schütt, 1896). Bütschli (1885) describe la placa romboidal '*Rautenplatte*' o primera placa apical. Stein, Bütschli y Schütt reconocían la importancia de la tabulación, es decir la disposición y forma de las placas tecales, como un valioso carácter taxonómico frente a otros caracteres secundarios como la ornamentación, pero no crearon un sistema para describir la tabulación.

En torno al cambio de siglo, Victor Hensen (1835-1924), organizó la '*Plankton-Expedition*' en 1889 con el objetivo de cuantificar el plancton en los océanos. Hensen había definido el concepto de plancton en 1887, reemplazando al *Auftrieb* de J. Müller. Su concepto de plancton correspondía a lo que hoy conocemos como seston, al incluir tanto partículas vivas como inertes. Poco después, Ernst Haeckel en su *Plankton-Studien* en 1890 limitaría el plancton a la

materia viva e introduciría términos muy comunes como ecología (inicialmente oecología), bentos, necton, nerítico, oceánico, meroplancton, holoplancton, etc.

Investigadores escandinavos como P.T. Cleve (1840-1905), Jørgensen (1862-1938), Ostenfeld (1873-1931) y Paulsen (1874-1947) realizan sus estudios principalmente en los mares del norte de Europa. En el Mediterráneo, un discípulo de Haeckel, Anton Dohrn (1840-1909), había fundado en 1872 la Stazione Zoologica de Nápoles. Los zoólogos centroeuropeos, Schütt, Schröder, Zimmermann o Schiller, veían Nápoles como un lugar con una diversidad casi tropical, pero seguro para su salud. Recordemos que en aquella época los muestreos en aguas cálidas acababan con los investigadores enfermos de malaria, cólera y otras enfermedades. Por ejemplo Ehrenberg había sido el único superviviente de una expedición a Libia y Egipto. En Messina y Sorrento, el fundador de *Archiv für Protistenkunde*, Richard Hertwig (1850-1937), describe *Leptodiscus* 1883 y *Erythropsis* 1884. Aún permanecía la idea de que muchos dinoflagelados no eran más que parte del ciclo de vida de otros organismos. En Villefranche-sur-Mer, el zoólogo Carl Vogt (1817-1895) criticaba duramente a Hertwig argumentando que *Erythropsis* no era más que *Vorticella* y que su ocelo era el ojo de una medusa que había ingerido.

Hasta entonces la bibliografía en alemán y francés dominaba los estudios de dinoflagelados. Charles A. Kofoid (1865-1947) comienza a investigar los dinoflagelados en California y aguas abiertas del Pacífico oriental. En su artículo sobre *Ceratium* ilustra las especies sin detalles en la forma y distribución de las placas tecales (Kofoid, 1907a), pero en un trabajo posterior sobre *Peridinium steinii* explica detalladamente un sistema de tabulación para Peridiniales, asignando un número dentro de cada fila de placas (Kofoid, 1909). La epiteca estaba dividida en dos series transversales completas: la apical (') y la precingular (''), contadas desde la posición ventral en el sentido contrario de las agujas del reloj. La hipoteca estaba también dividida en dos series: postcingular (''') y antapical ('''') (Fig. 14). Kofoid, con la ayuda de sus colaboradores, publicó una serie de monografías con detalladas ilustraciones de *Gonyaulax* (Kofoid, 1911), dinoflagelados atecados (Kofoid y Swezy, 1921), Dinophysiales (Kofoid y Skogsberg, 1929), *Heterodinium* (Kofoid y Adamson, 1933) y muchos otros trabajos (Kofoid, 1907b; Kofoid y Michener, 1911). Alrededor de unas 300 especies de dinoflagelados, hacen a Kofoid el autor más prolífico (Fig. 8). Sin embargo debe tenerse en cuenta que la mayor parte del trabajo lo realizaban

estudiantes. Entre sus colaboradores se encontraban mujeres como Josephine Michener y Olive Swezy. Con la excepción de Frances G. Whitting (Londres), Marie Victoire Lebour (1876-1971) en Plymouth y E. Catherine Herdman (1899-1953?) (no W.A Herdman) en Port Erin (Isla de Man), el estudio de los dinoflagelados estaba dominado por investigadores masculinos.

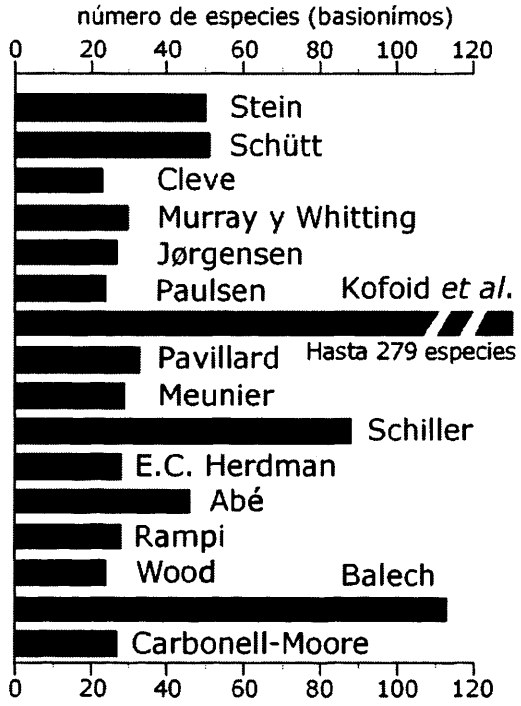


Fig. 8. Autores más prolíficos considerando el número de basionímos que describieron basado en Gómez (2005).

En la otra orilla del Océano Pacífico, Kintaro Okamura (1867-1936) comenzó los estudios de plancton en Japón (Omori, 2002) describiendo las primeras especies de dinoflagelados en la región. Tohru Abé (1899-1971) realizó una serie de minuciosos estudios de la tabulación, especialmente de las placas sulcales de Peridiniales y Dinophysiales (Abé, 1927, 1981). Los problemas de mareas rojas en aguas japonesas han sido estudiados por un numeroso grupo de expertos (Fukuyo, 1981). En China, Nie (1936) realiza estudios taxonómicos sobre algunos grupos.

En Francia hacia la década de 1880 existían Estaciones Marinas a lo largo de la costa mediterránea (Sète, Banyuls, Endoume y Villefranche) y atlántica (Concarneau, Wimereux, Roscoff). El príncipe Alberto I de Mónaco (1848-1922) patrocina algunas campañas oceanográficas y en 1910 funda el Museo Oceanográfico de Mónaco. Jules Pavillard (1868-1961) aprovecha esos recursos

para investigar los dinoflagelados principalmente en las costas francesas del Mediterráneo. En Sète y Banyuls, pero con frecuentes visitas a Roscoff y Wimereux, Édouard Chatton (1883-1947) realiza estudios citológicos y describe numerosos dinoflagelados parásitos con André Hollande (1913-1998) (Chatton, 1920). Entre sus discípulos se encontraba André Lwoff que consiguió el premio Nóbel de fisiología en 1965 (Soyer-Gobillard, 2002). En 1934, otra discípula de Chatton, Berthe Biecheler (1901-1939) usando el método de tinción de plata de Chatton y Lwoff (1930) observó la acrobase, delimitada por el 'apical groove' en inglés, y otras estructuras que serían visibles sólo años después con la microscopía electrónica. Los trabajos de Biecheler se truncaron por su prematura muerte y una parte de sus resultados los publicó P.P. Grassé (Biecheler, 1952). Los estudios citológicos de dinoflagelados continuaron en Banyuls con Marie-Odile Soyer-Gobillard, especialmente de la estructura del núcleo (Soyer, 1972). En Villefranche/Mer, Jean Cachon (1922-1989) y Monique Enjumet/Cachon-Enjumet/Cachon, describieron los sistemas de reproducción, percepción y locomoción, junto a contribuciones en el ciclo de vida de dinoflagelados parásitos y Noctilucales (Cachon, 1964; Cachon y Cachon, 1967, 1969). Otros investigadores en las costas mediterráneas francesas fueron P. Dangeard (1895-1970) en Banyuls, M. Travers en Endoume-Marsella y C. Greuet y G. Léger en Villefranche/Niza.

En Trieste, Josef Schiller (1877-1960) investigaba los dinoflagelados del Adriático y en 1931-1937 publica una revisión con ilustraciones y descripciones de los dinoflagelados, tanto marinos como epicontinentales, conocidos hasta entonces. La tradición taxonómica iniciada por los alemanes en Italia, continuaría con los italianos Raffaele Issel (1878-1936), Achille Forti (1878-1937) y Leopoldo Rampi (1905-1982) y hasta el presente especialmente en la Stazione Zoologica de Nápoles.

El primer microscópico electrónico se construyó en Berlín en 1931 por Ruska y Knoll. A partir de finales de los años 50 la microscopía electrónica comienza a incluirse en la descripción de dinoflagelados (Grell y Wohlfarth-Bottermann, 1957). La microscopía electrónica de transmisión permite detallados estudios de la estructura interna de los dinoflagelados (Dodge, 1968), mientras que la técnica de barrido permitiría conocer destalles de la superficie de las células, incluso de las especies más delicadas (Takayama, 1985).

En Argentina, Enrique Balech (1912-) usando microscopía óptica realiza detallados estudios de las placas sulcales y cingulares (Balech, 1980), del complejo del poro apical y de las placas antapicales (Balech y Tangen, 1985). Balech transfiere las especies marinas de *Peridinium* a *Protoperidinium*, el género más numeroso de dinoflagelados (Balech, 1974) y contribuye al conocimiento de géneros como *Alexandrium* (Balech, 1995). Balech y Abé se basaban en el laborioso estudio de las placas tecales, especialmente de las minúsculas placas sulcales. A menudo se solaparan en sus conclusiones como en el caso de la tabulación de *Dinophysis* (Balech, 1967; Abé, 1967). Abé de 1927 a 1941 publicó una parte de sus observaciones y después estuvo sin publicar durante 25 años. Durante esos años Balech publicó sus reformas de la tabulación de muchas especies, probablemente llegando a las mismas conclusiones a las que años antes había llegado Abé, pero que no había publicado. Entre 1966 y 1967 Abé publicó más resultados de sus viejos apuntes y a pesar de disponer de los trabajos de Balech publicados en español, en muchos casos ignoraba o quería ignorar los avances que Balech introdujó durante esos 25 años que Abé estuvo sin publicar. Por ejemplo cuando Balech le escribía recordándole que él ya había realizado modificaciones en la fórmula tabular de la familia Podolampadaceae, según Balech (1994) la respuesta de Abé fue: "*No tengo que entender español; acaso sabe Vd. japonés?*". Balech es, tras Kofoid y sus colaboradores, el autor más prolífico en número de especies descritas.

En el Océano Índico, Alain Sournia (1972a,b) y F.J.R. "Max" Taylor (1976) estudian la diversidad de dinoflagelados. Sournia (1973) revisa las nuevas entradas de especies posteriores a la revisión de Schiller y propone nuevas combinaciones en los nombres de especies con problemas en nomenclatura. En 1986, Sournia publica el *Atlas du Phytoplancton Marin* con ilustraciones y descripciones de todos los dinoflagelados marinos, pero sólo a nivel de género. Taylor (1987) edita una monografía sobre la biología de los dinoflagelados y en 1993 propone una clasificación conjunta de dinoflagelados vivos y fósiles (Fensome *et al.*, 1993), justo antes del comienzo de la aplicación de la biología molecular en la filogenia en dinoflagelados.

1.1.4. Los dinoflagelados en España[2]

Los exploradores españoles observaron numerosos fenómenos de mareas rojas y bioluminiscencia alrededor del mundo. En España, el fenómeno de las mareas rojas es frecuente en zonas de alta productividad biológica como las rías gallegas. A partir del siglo XIX ya estaban disponibles los primeros microscopios que permitían observar esos organismos hasta entonces invisibles. Era necesario el intercambio científico y tecnológico con los vecinos europeos para poder avanzar en el conocimiento de la diversidad marina. Sin embargo, tras la Revolución Francesa la monarquía española cerró las fronteras porque temía que junto al intercambio científico y cultural llegasen nuevas ideas que propiciasen una revolución con las consecuencias que tuvo para la monarquía francesa.

Las Ciencias Naturales eran necesarias para la explotación de los recursos naturales, pero su enseñanza era exclusivamente sistemática, memorística y no se incentivaba la investigación de laboratorio como las observaciones microscópicas. Llegaban nuevas ideas como las teorías evolutivas de Darwin publicadas en 1859, pero la Iglesia Católica, responsable de la enseñanza, consideraba peligrosas esas ideas que negaban la creación divina de los seres vivos. A partir de 1868, la situación política comenzó a ser más favorable al desarrollo y modernización de la ciencia y en 1871 se funda la Sociedad Española de Historia Natural.

Las actividades pesqueras y la explotación de los recursos marinos eran una prioridad y tan sólo hasta hace unas décadas España fue considerada la segunda potencia pesquera del mundo, sólo superada por Japón. A pesar del contexto de la época, el aislamiento en oceanografía no tenía sentido considerando que la explotación de los recursos marinos en aguas internacionales dependía de convenios entre naciones y los resultados científicos podían ser aprovechados por diferentes estados. España necesitaba acercarse al desarrollo de las actividades marítimas de los países europeos y tener Estaciones Marinas como nuestros vecinos franceses e italianos. Los primeros estudios científicos exploraron el desarrollo de la acuicultura en aguas gallegas (Graells, 1870), llegándose a proponer un centro de experimentación en acuicultura en la Bahía de Roses (Gerona). Las observaciones microscópicas de microalgas se restringían a diatomeas fósiles o especies epicontinentales (revisado en Azpeitia, 1911). J.

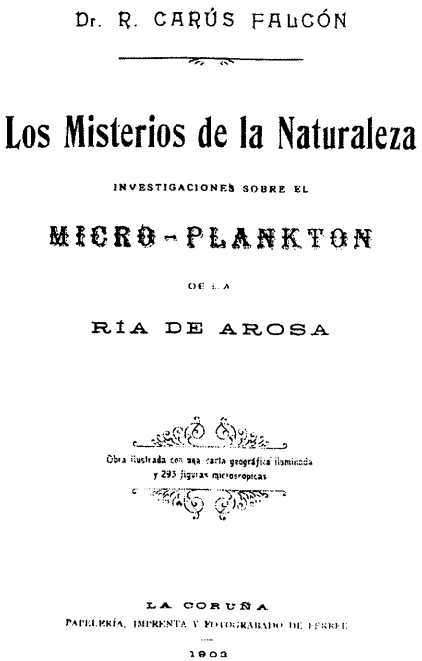
[2]Mi gratitud a Y. Pazos (Xunta de Galicia, Villagarcia de Arosa), S. Fraga (IEO, Vigo), M. Varela (IEO, A Coruña), J. Cort (IEO, Santander), A. García Calvo (Biblioteca, IIM, CSIC, Vigo) y J. Fonfrias (Univ. Complutense) por la bibliografía. Recomiendo la lectura del libro de S. Casado de Otaola (1997).

Puiggari en 1874 había publicado una lista de algunas diatomeas bénticas como *Nitzschia closterium* en aguas costeras de Barcelona.

El entomólogo Ignacio Bolívar (1850-1944), que digirió el Museo de Historia Natural desde 1901, se interesa por la biología marina y en 1881 publica un trabajo sobre los métodos usados en las campañas oceanográficas del Príncipe Alberto I de Mónaco. El teniente de navío J. de Borja visita la Stazione Zoologica de Nápoles y presentó su informe *Las colecciones zoológicas preparadas en Nápoles* al Ministro de Marina en 1891. El Ministerio de Fomento financia estancias en laboratorios europeos de naturalistas como el darvinista Augusto González de Linares (1845-1904) y José Rioja Martín (1866-1945). Por Decreto en 1886 se establece la creación de una Estación Marina y que se nombraría un director que debía elegir el lugar más apropiado de toda la costa española (Rioja y Martín, 1906; Sánchez, 1908). Antes, el Ministerio había enviado a su candidato, González de Linares, a estudiar la organización de la Stazione Zoologica de Nápoles (González de Linares, 1885). En 1887 nombran director al montañés González de Linares, quien elige Santander y nace la Estación Marítima de Zoología y Botánica Experimentales que después se denominó Estación de Biología Marítima de Santander (Madariaga, 1986). Al carecer de embarcaciones para la toma de muestras pelágicas y en una costa muy escarpada, los estudios se limitaron principalmente a invertebrados bentónicos y los pocos resultados apenas se publicaron. Según historiadores como Fraga Vázquez (2001) la escasa capacidad científica de su director y la falta de recursos financieros llevó a un escaso impulso científico. González de Linares dirigió la Estación de Biología Marítima hasta su muerte en 1904, reemplazado por su ayudante J. Rioja (Rioja y Martín, 1906).

El Ministerio de Fomento y el de Marina financiaron entre 1888 y 1893 el adiestramiento de 12 naturalistas y marinos en la Stazione Zoologica. Aunque antes de este impulso, el ingeniero Joaquín M. Castellarnau y de Lleopart (1848-1943) realizó una corta estancia en Nápoles en 1883 y en 1885 publica *La Estación Zoológica de Nápoles y sus procedimientos para el examen microscópico*. Anteriormente había publicado su *Teoría óptica del microscopio* en 1891. Ernesto Caballero (1858-1935), catedrático de Física de Pontevedra, había publicado su *Técnica de las preparaciones microscópicas sistemáticas* en 1897, e ilustró en una escala muy pequeña las diatomeas contenidas en los estómagos de ascidias de la Ría de Pontevedra.

La primera publicación incluyendo ilustraciones de dinoflagelados marinos, según mi conocimiento, se debió al esfuerzo individual y sin apoyo institucional. Roque Carús Falcón (1852-1910), médico y naturalista de Vilagarcía de Arosa (Pontevedra), disponía de un microscopio Zeiss y con una fina malla recogió muestras de plancton en sus excursiones en barco por la Ría de Arosa entre 1899 y 1901. En 1903 financia su libro *Los misterios de la naturaleza. Investigaciones sobre el micro-plankton de la Ría de Arosa* (Fig. 9) que llegó a ser traducida al alemán (Vila Fariña y Viana Martínez, 2001).


Dr. R. CARÚS FALCÓN

Los Misterios de la Naturaleza

INVESTIGACIONES SOBRE EL

MICRO-PLANKTON

DE LA

RÍA DE AROSA

Obra ilustrada con una carta geográfica iluminada y 295 figuras microscópicas

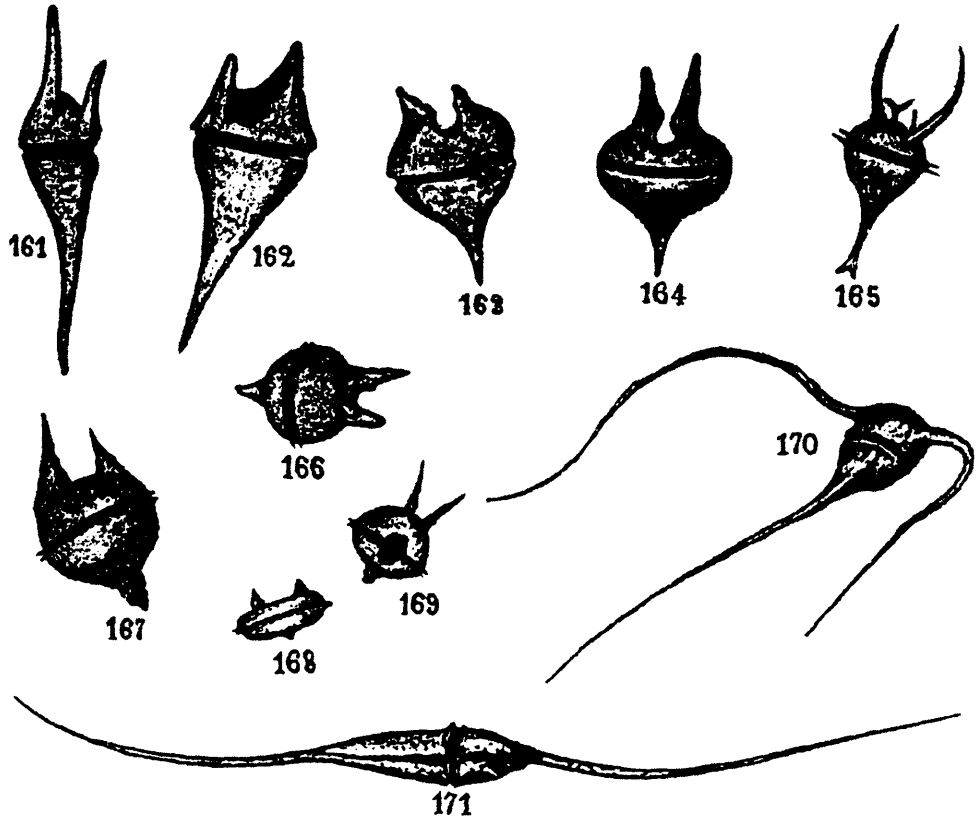
LA CORUÑA

1903

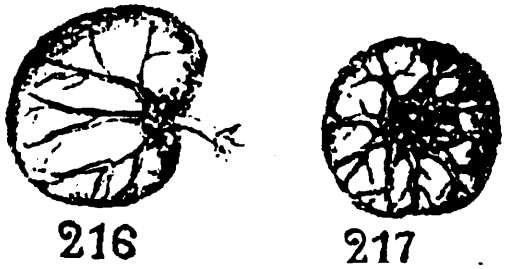
Fig. 9. Portada del libro de Carús Falcón (1903).

La primera descripción de dinoflagelados marinos en España comienza diciendo: "*Peridináceas. Los originales peridíneos, por otro nombre dinoflagelados, si bien se distinguen de las diatomeas por sus formas extravagantes, poco estéticas y feas...*" (Carús Falcón, 1903; p. 44). El autor carecía de las guías taxonómicas fundamentales en aquella época como Stein (1883), Gourret (1883) o Schütt (1895). Muy al estilo de la década anterior, ilustró los dinoflagelados con la epiteca hacia abajo. La primera especie citada fue *Ceratium furca* "ceratium furcus" y también observó *Ceratium fusus*. Ilustró un *Ceratium* con largos cuernos antapicales de distinta longitud que podría tratarse de *Ceratium trichoceros* o *C. buceros*, pero que Carús Falcón consideraba como una variedad de *C. furca* con tres 'flagelos'. Además ilustra 7 especimenes de *Protoperidinium*, dos de ellos podrían tratarse de *Protoperidinium divergens* (o *P. depressum*), al menos según su figura 164. Su figura 165 representaba un espécimen cuya hipoteca podría incluso corresponder a *Gonyaulax verior* con un larguísimo cuerno apical o más bien *Protoperidinium diabolus* o *P. longipes* con dos enfilados cuernos antapicales y unos extraños apéndices en la región antapical, quizás restos procedentes de otro organismo. Las figuras 166 y 167 se asemejan a la forma de un *Protoperidinium claudicans*,

mientras que la figura 168 muestra probablemente un *Protoperidinium ovatum* o *P. decipiens* y la 169 otra especie, bien con cuernos antapicales excesivamente alargados o el extremo apical roto. Carús Falcón muestra una tendencia a representar los apéndices más enfilados que en la realidad como en el caso de *C. fusus* (Fig. 10; su figura 171).



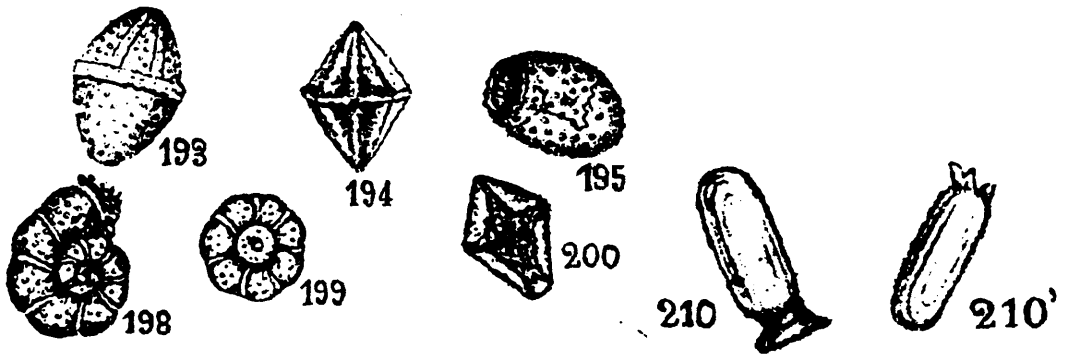
Peridíneos: 161, 162 y 170, variedades evolutivas de peridíneos del género ceratium furcus; 163, 164, 166, 167, 168 y 169, variedades del género peridinium; 165, forma rara, nueva y al parecer teratológica de los mismos; 171, peridíneo del género ceratium fusus.



—Protistos: 216 y 217 noctiluca miliaris.

Fig. 10. Ilustraciones de dinoflagelados en Carús Falcón (1903).

Carús Falcón ilustra *Noctiluca scintillans*, aunque no la incluye como dinoflagelado. Recordemos que *Noctiluca* no será considerada como un dinoflagelado hasta Kofoid (1920). Entre sus figuras de foraminíferos incluye ilustraciones que recuerdan a la forma de dinoflagelados (sus figuras 193, 194 y 200). Incluso su figura 210 se asemeja a la forma de *Dinophysis acuminata* (Fig. 11).



Protozoarios.—Foraminíferos: 191—196, 198—200, 206 y 209, conchas porosas de foraminíferos mono y politalamios; 201—205, foraminíferos radiolitos tri, tetra y exaradiados, agrupados según el orden evolutivo de perfectibilidad, en virtud de la selección natural ú otras causas; 197, 208, 207, 210—213, conchas lisas de foraminíferos, también mono y politalamios.

Fig. 11. Ilustraciones de foraminíferos según Carús Falcón (1903), pero que en algunos casos podrían corresponder a dinoflagelados.

Florentino Azpeitia Moros (1859-1934) en su libro publicado en 1911 *La Diatomología española en los comienzos del siglo XX* comentaba sobre las diatomeas del libro de Carús Falcón: "*sus figuras son tan deficientes, que en la mayoría de ellas no puede reconocerse ni aun el género...lo más prudente es prescindir en absoluto de esas citas...*". Sin embargo, las ilustraciones de diatomeas de Carús Falcón si que permiten reconocer las especies en la mayor parte de los casos, aunque sus identificaciones son a menudo incorrectas, por ejemplo confundiendo tintínidos de los géneros *Heliscostomella* y *Salpingella* con variedades de *Rhizosolenia styliformis*. Cuando Azpeitia publica su revisión en 1911, ni siquiera un género de diatomeas planctónicas tan común como *Chaetoceros* había sido citado por un autor español en nuestras costas. Con su esfuerzo Carús Falcón fue pionero en ilustrar el microplancton marino en España.

En 1886 uno de los estudiantes de González Linares, Odón de Buen y del Cos (1863-1945), había sido comisionado por el Ministerio de Fomento para realizar

trabajos oceanográficos en la fragata Blanca, buque escuela de los guardiamarinas españoles. Los resultados científicos fueron escasos porque el viaje se limitó a Europa y el norte de África y Buen, aún muy joven, carecía de suficiente experiencia (Buen, 1887). Buen visitó la Estación Zoológica de Villefranche/Mer, fue invitado al laboratorio Aragó en Banyuls/Mer y realizó campañas oceanográficas con el Prof. De Lacaze-Duthiers (1821-1901), fundador de la Estación Biológica de Roscoff en 1871 y Banyuls en 1882. Allí coincidió con uno de los fundadores de la oceanografía moderna. El príncipe Alberto I de Mónaco que había recibido su formación en la Marina Española, fomenta la cooperación internacional en materia oceanográfica en el Mediterráneo e introdujo a Buen en las organizaciones marítimas internacionales. Desde 1900, como profesor de Historia Natural en la Universidad de Barcelona, Buen fomentó los estudios prácticos llevando a sus estudiantes a muestreos costeros. En 1906 fundó la primera Estación Marina en la costa mediterránea española: el Laboratorio de Biología Marina de Porto Pí (Mallorca), del que fue nombrado director (Sánchez, 1908). A partir de 1912, ese laboratorio contaría con una sucursal permanente en Málaga, ambos centros ligados a la Universidad de Barcelona, como antesala de lo que más tarde sería el Instituto Español de Oceanografía fundado en 1914 (Parrilla-Barrera, 2005). Buen, que además era senador y concejal, había conseguido fondos para fundar el laboratorio en Baleares, algo que ya había intentado Bolívar, pero que no pudo conseguir al cambiar de signo el Gobierno en 1905 (Casado de Otaola, 1997). Bolívar hizo gestiones para crear un laboratorio en la costa norte de África en Magador, pero Buen desvió los recursos hacia un laboratorio en Melilla, que sólo llegaría a funcionar dos años por la inestabilidad política y militar en la zona.

En 1914, Buen funda el Instituto Español de Oceanografía, paradójicamente con sede en Madrid. Además de los laboratorios Porto Pí y Málaga, también al Instituto se adscribe el laboratorio de Santander. Eso significaba un cambio drástico en el modelo de uso de los laboratorios costeros, ya que el Instituto se centraba en las investigaciones sobre recursos de interés económico como las pesquerías y su prioridad no era la formación de investigadores, ni los estudios del plancton. Hasta entonces los cursos de formación en biología marina del Museo de Historia Natural se habían impartido en Santander, pero al pasar al Instituto los cursos tuvieron que darse en pequeños laboratorios provisionales en Valencia, A Coruña o San Vicente de la Barquera (Dosil Mancilla y Fraga Vázquez,

2001). Los investigadores y estudiantes del Museo de Historia Natural no tenían una salida al mar para desarrollar los estudios de biología marina. Los enfrentamientos llegaron a su grado máximo en 1917. Bolívar, que contaba con el apoyo del Real Sociedad de Historia Natural e incluso el personal del laboratorio de Santander, no consigue recuperar el laboratorio de Santander. Más tarde en 1919, el Museo de Historia Natural intentó sin éxito utilizar el Laboratorio de Hidrobiología de Valencia, pero no pudieron recuperar una salida al mar para sus investigadores hasta 1932. El Instituto alejado definitivamente de la Sociedad de Historia Natural, crea incluso su propia publicación en 1916 (Casado de Otaola, 1997).

Surgieron algunas iniciativas oceanográficas en ciudades litorales como San Sebastián con la creación de un Museo y un acuario. En Barcelona, la mayor ciudad en las costas españolas, también debía existir un laboratorio de biología marina. En 1917 se creo una sección oceanográfica en la Junta de Ciències Naturals de Barcelona (Casado de Otaola, 1997). En 1919 se publicó un folleto describiendo el proyecto del *Institut Oceanogràfic de Catalunya* en Barcelona que no llegaría a ejecutarse (comentado por Rioja, 1919).

Aunque los primeros laboratorios de biología marina no se crearon en las costas gallegas, la enorme productividad de esas aguas y fenómenos como las mareas rojas justificaban un mayor interés institucional. En vista de que el Museo de Ciencias Naturales no conseguía recuperar ninguno de los laboratorios costeros que pasaron al control del Instituto, decidieron crear un nuevo laboratorio. En 1920 Enrique Rioja Lo-Bianco, hijo del sucesor de González de Linares en el laboratorio de Santander, sugirió Marín en Pontevedra porque los problemas asociados a las fluctuaciones en las poblaciones de sardina y las mareas rojas, lo hacían más apropiado para formar a los jóvenes naturalistas. El Instituto Español de Oceanografía consiguió paralizar el proyecto y la Estación de Biología Marina de Marín no se fundó hasta 1932 (Martín y Rioja, 1933; Dosil Mancilla y Fraga Vázquez, 2001).

Las mareas rojas eran fenómeno muy común en verano en las Rías Bajas y no existían estudios científicos sobre el agente que las causaba. Por supuesto existían explicaciones populares para la *purga do mar* como la necesidad del mar de limpiarse o incluso que el mar '*menstrua*' (Sobrino, 1918). J. Murray (1885, p. 933) remarca la abundancia de *Noctiluca* en aguas del puerto de Vigo a finales de mayo de 1876, durante una escala del *Challenger* en su regreso a Inglaterra.

En 1887 Georges Pouchet y J. De Guerne publicaban sus análisis de las vísceras de sardinas procedentes de A Coruña. Entre otros organismos planctónicos, remarcaban una abundante cantidad de *Peridinium polyedricum* y *Peridinium divergens* Ehrenberg (=*Protoperidinium divergens*). *Peridinium polyedricum* Pouchet 1883 es ahora denominado *Goniodoma polyedricum* (Pouchet 1883) Jørgensen 1899 (no *Goniodoma polyedricum* Stein 1883). Georges Pouchet y J. De Guerne no ilustran estos dinoflagelados y alguna duda puede surgir en la identidad de *Peridinium polyedricum* Pouchet. Años antes, Pouchet (1883, fig. 34) había descrito esa especie a partir de muestras de Concarneau y Marsella, pero su ilustración no incluía la vista ventral. La tabulación y el contorno de la célula en vista dorsal de la descripción original no coinciden con *Gonyaulax polyedra* Stein 1883, pero no hay que descartar que las sardinas hubiesen ingerido *Gonyaulax polyedra*.

En 1916 como solía ocurrir cada verano las aguas de las Rías Bajas se volvieron a colorear de un tono rojizo. Un pontevedrés, Ramón Sobrino Buhigas (1888-1946), entonces profesor en el Instituto de Pontevedra y director del Museo de Historia Natural de Pontevedra, aun careciendo de un buen microscopio se interesó por el fenómeno. En un periódico local (*La Correspondencia Gallega*, 7 Julio 1916) Sobrino relataba "*siendo al parecer el Ph. pouchetii la especie que accidentalmente se encuentra en las aguas de nuestra ría y a la que acompañan otras pertenecientes a los géneros Pyrocystes, y Noctiluca*". Quizás Sobrino había leído sobre las proliferaciones de *Phaeocystis* en el Canal de la Mancha y el Mar del Norte y extendió el fenómeno a las costas gallegas y también atribuyó la bioluminiscencia a *Noctiluca* como tradicionalmente se venía haciendo. Por tanto parece que Sobrino más que en rigurosas observaciones al microscopio se basaba en lo que podría ser según ejemplos de la bibliografía.

Por otro lado, Buen también interesado por el fenómeno había tomado muestras ese mismo verano en las Rías Bajas a bordo del *Hernán Cortés* equipado con un microscopio binocular Zeiss (Buen, 1916a). Según Buen: "*el microscopio ha revelado que el autor de ese color ocráceo es un protoorganismo del grupo de los radiolarios*" y también comentaba "*haber observado intensa producción de estos interesantes animales en las Salinas de Mallorca*" (Buen, 1916b, p. 6, 9). Ni Sobrino ni Buen en sus observaciones microscópicas identificaron al agente causante de la marea roja porque ni *Phaeocystis* prolifera

en verano en Galicia ni colorea el agua de un tono rojizo, ni tampoco los radiolarios producen mareas rojas en ningún lugar del mundo, ni en Galicia ni en las salinas de Mallorca. Ambos autores indicaban la presencia de *Noctiluca*, que si bien puede producir una coloración anaranjada-púrpura, no debía ser el responsable primario de la marea roja. *Noctiluca* es un dinoflagelado heterótrofo de gran tamaño que requiere para su proliferación grandes cantidades de presas como diatomeas o dinoflagelados autótrofos, que si son el origen primario de una marea roja.

Al verano siguiente en 1917, Sobrino ya disponía de un moderno microscopio Leitz y la marea roja volvió. Con la ayuda de E. Caballero realizó fotomicrografías que mostraban una densa proliferación de *Lingulodinium* (=*Gonyaulax*) *polyedra.* Sus ilustraciones incluían incluso detalles como el poro ventral en la primera placa apical (Fig. 12). Sobrino (1918) ilustra la tabulación, aunque sin usar el sistema propuesto por Kofoid en 1909. Otros dinoflagelados presentes durante la marea roja eran *Ceratium fusus*, *C. furca*, *Prorocentrum micans* y dos especies de *Protoperidinium*, *P. divergens* y probablemente *P. steinii*. El hecho de que Sobrino usase "*Ceratium divergens*" y "*Ceratium Michaelis*" para referirse a dos especies de *Protoperidinium*, no es ningún error suyo. Sobrino tan sólo estaba siguiendo las desafortunadas modificaciones introducidas por W. Saville Kent en su popular *Manual of the Infusoria* de 1881-1882. La ilustración de un dudoso "*Ceratium Michaelis*" es poco acertada, no recuerda a *P. steinii* Jørgensen e incluso se asemeja a *Podolampas bipes* (Fig. 12). Sobrino también cita los géneros *Polykrikos*, *Dinophysis* y *Noctiluca.*

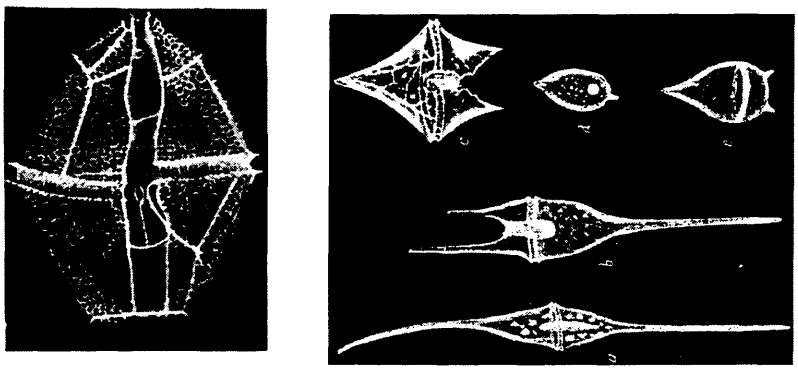


Fig. 12. Ilustraciones de *Gonyaulax polyedra, Ceratium fusus, C. furca, 'Ceratium divergens', Prorocentrum micans y 'Ceratium Michaelis'* por Sobrino (1918).

El agente causante de la marea roja estaba claro, al menos en el puerto de Marín aquel verano de 1917. Pocos meses después Sobrino publicó los resultados con el título de *La purga de mar o hematotalasia*. Sin duda realizó un buen trabajo taxonómico identificando correctamente a *Lingulodinium polyedra*, pero más discutible resultan sus argumentos para relacionar el fenómeno de las mareas rojas con la biología de la sardina, monopolio del recién creado Instituto Español de Oceanografía. Sobrino (1918, p. 412) reconoce su error al considerar a *Phaeocystis* como responsable de la marea roja en 1916. Sin embargo, el Instituto Español de Oceanografía, lejos de reconocer su error al considerar que un radiolario fue responsable de la marea roja en las Rías Bajas en el verano de 1916, replica duramente a Sobrino. Fernando de Buen (1918, p. 328) sale en defensa de su padre argumentando "*yo he podido ver, y hemos preparado, abundantes radiolarios, acompañados de escasas peridíneas del plankton recogido durante el verano de 1916, cuando se presentaba la coloración. Al año siguiente, o sea en el verano de 1917, los radiolarios desaparecieron casi por completo. El abundante material de que dispone el Instituto asegurara siempre nuestras afirmaciones con datos perfectamente comprobables*". Fernando de Buen en su réplica a Sobrino alardea del abundante material y recursos de los especialistas del Instituto, pero no proporciona ningún dato como una ilustración o el nombre del supuesto radiolario responsable de la marea roja de 1916, y ni siquiera da resultados de las muestras recogidas en el verano de 1917. Sobrino, tras resolver que el agente causante de la marea roja era un dinoflagelado, al menos en aquel caso, continuaría su labor como profesor de Ciencias en la Universidad de Santiago de Compostela. Dos décadas más tarde, un estudiante de Sobrino sería el primer español en describir nuevas especies de dinoflagelados.

El Instituto Español de Oceanografía realizaba campañas, se tomaban muestras, pero no se publicaban resultados. El primer laboratorio del Mediterráneo, fundado en 1906, no realizó sus primeros estudios de plancton hasta 1928 (Navarro y Massutí, 1929). Miguel Massutí Alzamora, ayudante del Laboratorio de Biología Marítima de Porto Pí, publicó una lista de dinoflagelados en la Bahía de Palma en 1929, pero explica "*No habiéndome sido posible su estudio con la detención deseada, me limito a las breves notas que siguen, ya que nuestro compañero Doctor Cuesta, del Laboratorio de Santander, tiene en estudio las peridinias de nuestras muestras*" (Massutí, 1930). Juan Cuesta

Urcelay (1897-1970) recibía las muestras de plancton de las campañas del Instituto Español de Oceanografía, pero o no las analizaba o no publicaba los resultados. Hasta Navarro y Massutí (1929) el Instituto no publica listas de especies fitoplanctónicas.

En 1906 Santiago Ramón y Cajal (1852-1934) había recibido el premio Novel tras desarrollar una tinción con nitrato de plata para el estudio del sistema nervioso. La histología española alcanza un gran desarrollo y sucesores del premio Nóbel, Achúcarro y Río-Hortega, habían creado variantes del método. Investigadores del Instituto Español de Oceanografía como Sánchez y Sánchez (1919) y Cuesta (1919a) siguen la moda de la época y explican como aplicar el método a los organismos planctónicos. Cuesta (1919b) observa estructuras como los cirros o tricocistos (eyectisomas),

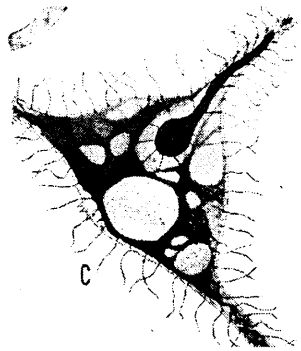


Fig. 13. Detalle de la ultraestructura de *Ceratium* por Cuesta (1919b).

Cuesta también aplica el método de Río-Hortega al estudio del núcleo de especimenes de *Ceratium* y *Peridinium*. Cuesta (1921, p. 371) comentaba "*El núcleo de Peridinium en su estado de reposo deja difícilmente ver la membrana; la cromatina no se presenta bajo la forma típica en esta clase de seres (principalmente* Ceratium*)*" y "*No en todos los ejemplos anteriormente expuestos se comporta igualmente la membrana nuclear: mientras en unos casos, como las figs. I, 2, 9, etc., persiste, en otros, como en las 6, 7 y 8, aquella desaparece*" (Cuesta, 1921, p. 374). La membrana nuclear en dinocariontes es persistente y no existen diferencias significativas entre los núcleos de *Ceratium* y *Peridinium*. Al menos Cuesta estuvo más acertado al remarcar la falta de centríolos en *Ceratium*, contrariamente a algún estudio anterior. Estas observaciones en la ultraestructura no llegaban al nivel de los estudios de Chatton en Banyuls y su discípula Biecheler (1934) en su "*Sur le réseau argentophile et la morphologie de quelques Péridiniens*". Cuesta Urcelay en poco contribuía al estudio del fitoplancton, el sistema del Instituto Español de Oceanografía no formaba ni

reclutaba especialistas en fitoplancton y había privado a los naturalistas de laboratorios costeros donde formarse e investigar.

En el otoño de 1928 el danés Ove Paulsen realiza una estancia en el laboratorio de Málaga invitado por O. de Buen. Paulsen entrega sus resultados sobre el microplancton en las costas de Málaga en 1930 (publicado en 1931), incluyendo la descripción de nuevas especies de diatomeas. También describe *Ceratocorys kofoidii* Paulsen 1931, un nuevo dinoflagelado que es un sinónimo de *C. gourretii*. Paulsen discute sobre la enrevesada sinonimia de *Ceratocorys gourretii* y posteriormente Schiller (1937, p. 446) atribuiría la especie *Ceratocorys gourretii* a Paulsen, siendo *Dinophysis jourdanii* Gourret su basionímo. A partir de especimenes de la costa de Málaga, Paulsen propone *Peridinium simulum* separándolo del fondo de saco en que se había convertido *Peridinium globulus* Stein. Un caso similar fue *Peridinium marielebouriae* que Paulsen considera como una de las ilustraciones de Lebour (1925) bajo el nombre de *P. obtusum* Karsten. En apenas unas semanas de muestreos costeros y ya pasado el verano, Paulsen tan sólo pudo investigar una pequeña parte diversidad de dinoflagelados del Mar de Alborán, pero realizó el trabajo más completo sobre fitoplancton en las costas españolas hasta la fecha. Cuando Schiller (1931-1937) publica su revisión sobre dinoflagelados no cita ninguna contribución de un autor español, aunque al menos el trabajo de Sobrino (1918) debió incluirse.

El primer español en describir una especie de dinoflagelado, aunque lamentablemente fuera de España, tendría que ser otro pontevedrés. El alcalde de Pontevedra, el polifacético Bibiano Fernández Osorio-Tafall (1903-1990), discípulo de Sobrino y profesor del Museo de Historia Natural de Pontevedra, realiza estudios sobre el fitoplancton en la Estación de Biología Marina de Marín que funcionó entre 1932 y 1935. Ayudado por E. Caballero, publica sus primeros trabajos sobre diatomeas. Osorio-Tafall (1936) cita en su trabajo a *Lingulodinium polyedra*, *Prorocentrum micans* y *Ceratium furca* como las especies de dinoflagelados dominantes en las Rías Bajas en agosto. No parece que le diera tiempo a publicar sus resultados sobre dinoflagelados, cuando el desenlace de la Guerra Civil obliga al exilio de muchos científicos españoles. Odón de Buen, al igual que sus hijos Fernando y Rafael y muchos otros de esos primeros oceanógrafos y naturalistas se exiliaron a países como México. En el exilio, Osorio-Tafall describió varias especies de dinoflagelados en el Golfo de California:

Ceratocorys allenii (=*C. gourretii*), *Parahistioneis pieltainii*, *Prorocentrum mexicanum*, *Prorocentrum robustum* y *Prorocentrum veloi* (Osorio-Tafall, 1942a). También describió *Lophodinium dadayi* (=*Lophodinium polylophum*) en aguas epicontinentales (Osorio-Tafall, 1942b).

Medio siglo tras los primeros viajes de adiestramiento a Nápoles, no existía una tradición en estudios taxonómicos de dinoflagelados y nunca se llegó a formar a un fitoplanctólogo marino o al muestreo en aguas oceánicas. Además de los pocos recursos disponibles para investigación, las disputas entre el Instituto Español de Oceanografía y el Museo de Historia Natural en poco habían favorecido el desarrollo de los estudios de fitoplancton. Margalef (1947) evaluaba la contribución de los centros de Santander, Mallorca y Marín concluyendo "*estas instituciones se han limitado especialmente al estudio de las aguas costeras y la labor realizada sobre el plancton ha sido poco considerable*". La Guerra Civil había supuesto la pérdida de científicos, por ejemplo un prometedor Osorio-Tafall, pero por otro lado había terminado con la disputa Instituto Español de Oceanografía y el Museo de Historia Natural, que sin duda se hubiese perpetuado por más tiempo. El vacío creado por el exilio de los primeros científicos marinos, pudo liberar de posibles ataduras conceptuales y permitir que miembros de la siguiente generación pudiesen desarrollar sus ideas con un enfoque libre, como así ocurriría con un excepcional desarrollo en el campo de la ecología. Tras la guerra civil, nuevos investigadores debían surgir, pero como antes principalmente debido al talento individual y con escaso apoyo institucional.

A partir de 1945, Ramón Margalef López (1919-2004) comienza a publicar sus estudios sobre el fitoplancton en las costas españolas (Margalef, 1945) y aparece la primera guía de identificación de fitoplancton (Massutí y Margalef, 1950). Margalef describe los géneros *Scaphodinium* 1963 y *Ceratoperidinium* 1969 en la costa mediterránea, las especies *Cochlodinium polykrikoides* 1961 y *Peridinium volsella* 1968 (fechado 1965) en el Mar Caribe y propone nuevas combinaciones como *Ceratium furca* var. *hircus* (Schröder) Margalef y *Micracanthodinium quadrispinum* (Pavillard) Margalef. Varias especies de dinoflagelados se dedicarían a Margalef: *Peridinium margalefii* E.S. Silva 1965, *Oxytoxum margalefii* Rampi 1969, *Pyrocystis margalefii* Léger 1973, *Ceratoperidinium margalefii* Loeblich III 1980, *Alexandrium margalefii* Balech 1994 y *Scrippsiella ramonii* Montresor 1995. Margalef publicaría trabajos sobre la composición del fitoplancton marino con investigadores como E. Morales, J.

Herrera, M. Durán, A. Ballester, J. Castellví y M. Estrada. López (1955) investiga la morfometría de *Ceratium* en Castellón y Balle (1953) realiza estudios sobre la composición del fitoplancton de las campañas del laboratorio de Porto Pí.

Margalef (1956) también se interesa por las mareas rojas en Galicia. La gran producción acuícola gallega, especialmente de mejillón, comenzaba a exportarse y casos de intoxicaciones motivaron un mayor interés institucional. La especie tóxica *Gymnodinium catenatum* se detectó en aguas gallegas (Estrada *et al.*, 1984). Este esfuerzo en el seguimiento de las especies tóxicas lleva a describir *Gyrodinium impudicum* Fraga *et* Bravo 1995, una especie inocua, pero morfológicamente cercana a *G. catenatum* (Fraga *et al.*, 1995). También se investiga el ciclo de vida de *Dinophysis* (Reguera *et al.*, 1995), los quistes recientes de dinoflagelados (Blanco, 1989) y los factores ecológicos relacionados con las mareas rojas (Figueiras y Pazos, 1991). El Centro Oceanográfico de Vigo creado en 1972 acoge al Centro Científico y de Comunicación sobre Algas Nocivas, fruto de un acuerdo de colaboración entre el Instituto y la Comisión Oceanográfica Intergubernamental de la UNESCO. Este Centro mantiene cultivos de referencia de especies tóxicas e imparte cursos de formación a investigadores. En A Coruña, el Instituto realiza muestreos radiales en aguas abiertas gallegas y del Mar Cantábrico (Varela, 1982).

Tras el frustrado intento de *Institut Oceanogràfic de Catalunya* en 1919, desde 1951 el Instituto de Ciencias del Mar de Barcelona dependiente del Consejo Superior de Investigaciones Científicas es el centro con el mayor número de investigadores en ciencias marinas de España. Sus investigadores realizan estudios sobre la composición del fitoplancton (Estrada, 1979; Delgado y Fortuño, 1991), principalmente centrados en aspectos ecológicos y especies tóxicas (Garcés *et al.*, 1998; Vila *et al.*, 2001).

En Canarias Ojeda (1999) investiga los dinoflagelados subtropicales. Aparecen trabajos dispersos en taxonomía de dinoflagelados como la descripción de *Peridiniopsis salina* en aguas salobres de la Ría de Bilbao (Trigueros, 2000). Otros autores realizan estudios citológicos y genéticos de dinoflagelados (Costas y Varela, 1988; Zardoya *et al.*, 1995; Costas y Goyanes, 2005).

1.1.5. La biología molecular en la última década

Además de la taxonomía más clásica basada en la morfología de las especies, ha surgido en la última década una nueva herramienta basada en la secuenciación de diversas regiones del genoma en los estudios de dinoflagelados.

En 1977 se completó la primera secuencia de nucleótidos del genoma de un bacteriófago (Sanger *et al.*, 1977). Hinnebusch *et al.* (1981) determinaron parcialmente la secuencia de nucleótidos del rARN 5 y 5.8S de *Crypthecodinium cohnii* y la compararon con organismos superiores. La técnica era muy laboriosa aún, pero en Banyuls siguiendo la tradición iniciada por Chatton, colaboradores de M.O. Soyer, secuenciaban algunos genes de pequeño tamaño de *Prorocentrum micans* y continuarían sus trabajos en Estados Unidos (Maroteaux *et al.*, 1985; Herzog y Maroteaux, 1986). Las primeras secuencias de nucleótidos comenzaban a estar disponibles en las especies *Crypthetodinium cohnii* ac#M53134, M23736 y *Prorocentrum micans* ac#M03538. Mullis en 1983 concibe una técnica más rápida y fácil de amplificar el ADN con la reacción de polimerización en cadena (PCR) (Saiki *et al.*, 1985) y el número de secuencias de dinoflagelados disponibles se incrementa, principalmente a partir de las especies disponibles en cultivos.

El genoma de un dinoflagelado es unas 100 veces mayor que el humano y se deben seleccionar las regiones de interés. La secuencia del ADN ribosómico (rADN) que codifica el rARN es la más comúnmente usada para realizar comparaciones filogenéticas dada su universalidad al encontrarse en los genomas procariotas, eucariotas, del cloroplasto y de la mitocondria. El rADN codifica para la subunidad pequeña (SSU rARN), y a ambos lados del 5.8S rADN se encuentran las secuencias de las regiones intergénicas (ITS1 e ITS2; "*internal transcribed spacer*") y la subunidad grande (LSU rARN). Los genes del ARN ribosómico (18S, 5.8S y 28S) son conservativos, con múltiples copias en el genoma y sus secuencias son suficientemente variables entre las especies como para permitir comparaciones válidas estadísticamente. Para reconstrucciones filogenéticas deben usarse las regiones más conservadas y con una tasa moderada de cambios para evitar que fenómenos con la transferencia lateral de genes o simplemente las mutaciones afecten a las conclusiones. La subunidad pequeña (SSU rARN) sería la región más apropiada, mientras que subunidad grande (LSU rARN), especialmente sus dominios D1/D2, 5.8S rADN y regiones intergénicas (ITS1 e ITS2) son más variables (Scholin *et al.*, 1993). Las secuencias de las

regiones intergénicas (ITS1 e ITS2) son variables incluso en la misma especie, permitiendo comparar variaciones genéticas de especímenes procedentes de diferentes regiones y establecer relaciones biogeográficas.

Los primeros estudios filogenéticos, basados en *Crypthetodinium cohnii*, mostraban antecesores comunes para los dinoflagelados y los Apicomplexa, parásitos como *Plasmodium* que produce la malaria y muy próximos filogenéticamente a los ciliados (Gajadhar *et al.*, 1991; Wolters *et al.*, 1991). Todos ellos se agruparon en el grupo denominado Alveolata, que tienen en común los alvéolos corticales: sacos o vesículas aplanadas que sostienen la membrana plasmática que reciben el nombre de anfiesma en dinoflagelados. Esos primeros estudios mostraron que los Gymnodiniales y Prorocentrales aparecieron más recientemente a partir de los Peridiniales y que las especies autótrofas surgieron a partir de heterótrofas (Lenaers *et al.*, 1989, 1991).

La biología molecular aparece como una nueva herramienta a la hora de diferenciar entre especies de *Alexandrium*, ya que especies tóxicas o inocuas de este género son difíciles de diferenciar morfológicamente. En *Alexandrium catenella* se secuenció la región 18S (Destombe *et al.*, 1992), los dominios D1/D2 del 28S rADN (Scholin *et al.*, 1994) y la región intergénica ITS y 5.8S (Adachi *et al.*, 1994, 1996). Una vez establecida la secuencia de fragmentos específicos de ADN de la especie tóxica, se pueden diseñar sondas de oligonucleótidos (15-50 nucleótidos), principalmente con marcadores fluorescentes, que permita detectar las especies de interés incluso por no especialistas en taxonomía. Por otro lado, en lugar de tratar de detectar una especie cuya secuencia ya es conocida, también se pueden añadir cebadores '*primers*' de una secuencia común en todos los dinoflagelados. De esta forma se amplifican secuencias sin tener ninguna referencia de la morfología de la especie. Sólo si la secuencia obtenida coincide con alguna secuencia registrada en los bancos de ADN, se puede establecer a que especie puede corresponder. Es una filogenia 'a ciegas', aportando la secuencia de ADN del dinoflagelado y desconociendo su morfología, pero que revela información sobre una gran diversidad de especies por conocer (López-García *et al.*, 2001). En esta filogenia 'a ciegas' hay que tener precaución porque errores en las replicaciones o mutaciones en los genes repetidos pueden dar lugar a confusiones que lleven a sobreestimar la diversidad genética.

A medida que las secuencias disponibles aumentan en librerías genómicas accesibles en Internet (GenBank), empiezan a buscarse caracteres morfológicos que son comunes en especies que aparecen próximas en los árboles filogenéticos. La técnica se ha aplicado al género *Gymnodinium* que incluía más de doscientas especies. *Gymnodinium* se ha escindido en 5 géneros basados en la combinación de biología molecular, composición pigmentaria y caracteres morfológicos, como la forma del surco apical (Daugbjerg *et al.*, 2000). En ocasiones, pequeñas diferencias en la secuencia se han usado para separar especies, pero queda definir cuantos nucleótidos diferentes y en que parte del genoma justifican la separación como especies diferentes.

La mayoría de los estudios filogenéticos se basan en abundante material a partir de cultivos. Sin embargo, son pocas las especies de dinoflagelados fácilmente cultivables. A principios de este milenio, se describen técnicas que parecen solucionar este problema al permitir aparentemente obtener las secuencias a partir de un solo espécimen o un quiste, incluso fijados (Bolch, 2001; Marín *et al.*, 2001; Ruiz Sebastián y O'Ryan, 2001). Por tanto, todo hacía esperar que muy pronto las secuencias de la mayor parte de las especies estuvieran disponibles. Aún en la actualidad, la probabilidad de obtener la secuencia a partir de una sola célula es baja y es necesario tener más de un espécimen, por lo que parece que se exageraban las virtudes del método conocido como *single-cell PCR*. Apenas están disponibles secuencias de unas 100 especies de dinoflagelados (Murray *et al.*, 2005). Hay además un gran sesgo hacia las especies cultivables o fácilmente accesibles en aguas costeras, es decir, especies autótrofas de los géneros *Alexandrium*, especies cercanas a *Gymnodinium* y otros grupos que forman grandes proliferaciones costeras. En el presente, la biología molecular aún no ha sido aplicada a la gran diversidad de dinoflagelados oceánicos y temas de investigación como la especiación críptica está en sus comienzos.

1.2 ¿Qué son los dinoflagelados?

Es difícil definir una característica común a todos los dinoflagelados sin que aparezcan excepciones. A alguien que observa por primera vez una muestra de microplancton con un microscopio a 200 o 400 aumentos, se le podría decir que los organismos con formas geométricas y cristalinas son las diatomeas y los dinoflagelados aparecen con formas más irregulares ó como decía Carús Falcón (1903): '*formas extravagantes, poco estéticas y feas*'. Si la muestra esta fijada con Lugol, la celulosa que compone las tecas de los dinoflagelados se teñirá de un color marrón. En algunas células se puede observar el flagelo transversal ondulado, sobre todo si esta desprendido del cíngulo, pero muy raramente el flagelo longitudinal que normalmente se pierde al fijar las células. Si se tiene la oportunidad de observar dinoflagelados vivos, su desplazamiento rotando sobre sí mismos es muy distintivo y da nombre al grupo. El tamaño del núcleo, siendo visible la cromatina, sorprende cuando se compara con otros grupos fitoplanctónicos como las diatomeas.

Como productores primarios, aproximadamente la mitad de las especies de dinoflagelados son fotosintéticos, contribuyendo a los ciclos biogeoquímicos en los océanos como otras microalgas. En términos de riqueza de especies, según Sournia *et al.* (1991) existen 1700 especies de dinoflagelados marinos y un número similar de diatomeas planctónicas marinas, y desde este punto de vista sería el grupo más importante del fitoplancton marino por su riqueza de especies.

Los dinoflagelados tienen características similares a otros grupos de protistas, pero en los siguientes apartados se describen aquellas características distintivas y en muchos casos únicas que sólo pueden encontrarse en dinoflagelados.

1.2.1. Células móviles

Los dinoflagelados presentan una gran variedad de formas en su ciclo de vida con formas aflageladas (cocoides, filamentosas, quistes palmeloides o ameboides), pero la mayor parte de las especies son biflageladas al menos en alguna parte del ciclo de vida. Por ejemplo, *Pfiesteria piscicida* en los estuarios norteamericanos muestra hasta 24 morfologías diferentes combinando células flageladas y ameboides en 3 ciclos de vida (Burkholder *et al.*, 1995).

Las células móviles, llamadas mastigotas, suelen tener dos flagelos (undulipodium), uno transversal ondulado que bate en múltiples ondas y otro

flagelo longitudinal. El margen por el que emergen los dos flagelos se define como ventral y el opuesto como dorsal (Fig. 14). Según la posición de los flagelos, los dinoflagelados se han divido en: células dinocontas cuando los flagelos se insertan ventralmente y un grupo menos numeroso, células desmocontas, en la que los flagelos se alojan en la zona anterior como en el caso de *Prorocentrum* con dos grandes placas laterales. En este caso, Bütschli (1885) estableció que la valva excavada que contiene el área periflagelar sería la valva derecha. Sin embargo, algunos autores han revertido esta orientación desconociendo que ya fue establecida. En otros casos, ambos flagelos son posteriores como en *Torodinium*, denominándose células opistocontas.

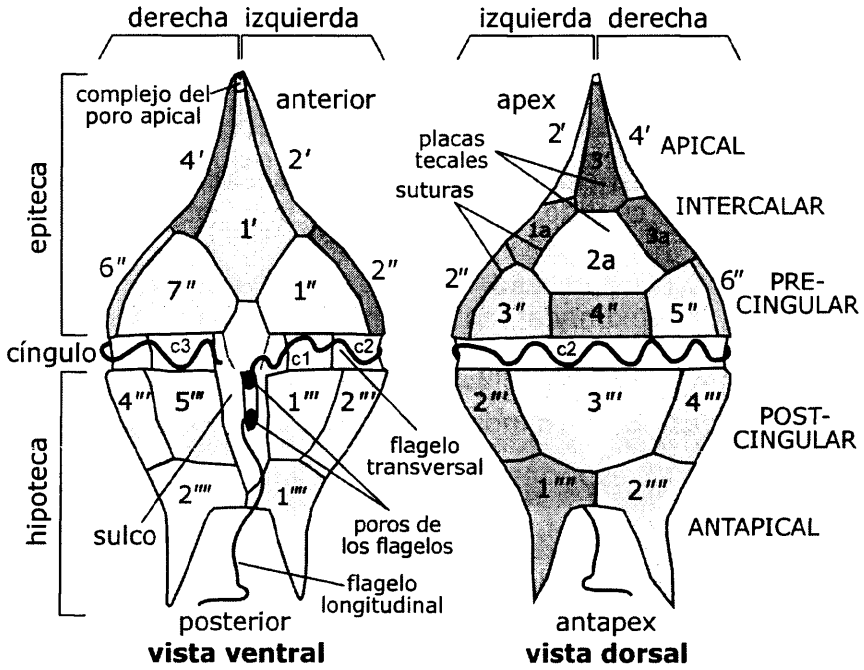


Fig. 14. Esquema simplificado, terminología y tabulación de un dinoflagelado tecado tipo usando como ejemplo un *Protoperidinium*: Po, X, 4', 3a, 7", (3+t)c, 6s, 5"', 2"".

1.2.1.1. Flagelo transversal y orientación

Los dinoflagelados se caracterizan por poseer un flagelo transversal alojado en una hendidura o surco transversal que rodea a la célula y recibe el nombre de cíngulo. Este tipo de flagelo ondulado es distintivo de dinoflagelados y tan sólo se ha encontrado también en crisófitas pedineloides. El flagelo transversal es también único al presentar mastigonemas. El flagelo se bate en múltiples ondas y permite la rotación sobre el eje longitudinal de la célula (Fenchel, 2001), pero también su propulsión (Gains y Taylor, 1985). El cíngulo (región mesómera) divide a las células dinocontas en una parte anterior llamada episoma (también hipocono y epiteca en dinoflagelados tecados, región acrómera y prosómera) y la

parte posterior llamada el hiposoma (hipocono o hipoteca, región opistómera). En células desmocontas faltan el cíngulo y sulco y por tanto la célula no se divide en epiteca e hipoteca, sino valva derecha o izquierda. Las Noctilucales tienen su propia orientación establecida por Cachon y Cachon (1967, 1969), en algunas especies uno de los flagelos está ausente o es vestigial y en otras especies el flagelo aparece encapsulado en su parte proximal.

El cíngulo es planar cuando las terminaciones de la parte proximal y distal están alineadas. Normalmente una de las terminaciones es más anterior que la otra, y ese desplazamiento se mide en términos de anchuras de cíngulo. El desplazamiento y la 'torsión' incrementan la longitud del flagelo transversal y se especula que su potencia locomotora (Gains y Taylor, 1985). El flagelo transversal se orienta hacia la izquierda, en sentido contrario a las agujas del reloj. El cíngulo es laevorotatorio (también llamado descendente o sobre izquierda, terminación proximal) o dextrorotatorio (ascendente o sobre la derecha, terminación distal). Por consenso, el lado derecho e izquierdo se determina como en humanos. Se debe prestar especial atención porque los sistemas ópticos pueden dar una imagen especular o en casos de células muy aplanadas se puede estar focalizando en la parte de atrás. Los mastigotos suelen ser asimétricos y la parte izquierda tiende a estar más desarrollada que la derecha, como ocurre en la aleta sulcal izquierda de los Dinophysiales.

1.2.1.2. Flagelo longitudinal y desplazamiento

El otro flagelo es similar al que se puede encontrar en la mayor parte de microalgas. Es acronemático (liso y terminado en una fina fibrilla), cilíndrico o aplanado y nunca más grueso que el flagelo transversal. El flagelo longitudinal es normalmente perpendicular al cíngulo y la parte proximal se aloja en una hendidura o surco que recibe el nombre de sulco. El sulco interrumpe el cíngulo en la parte ventral y a veces invade la epiteca. Además del cíngulo y sulco, otros surcos pueden aparecer en la superficie de la epiteca (excepcionalmente en la hipoteca como en *Amphidinium carterae*) recibiendo el nombre de surco apical o 'apical groove' en inglés, que delimita la acrobase. El surco apical, a pesar de no estar conectado con el sulco, puede considerarse una extensión de éste en la epiteca.

El flagelo longitudinal vibra con menor frecuencia que el flagelo transversal y propulsa posteriormente a la célula y permite cambiar la orientación. Con la combinación del movimiento de ambos flagelos, el dinoflagelado se desplaza

describiendo una trayectoria helicoidal en sentido horario que puede ser considerado como un mecanismo de orientación en un gradiente químico (helicoidal clinotaxis). Por consenso, el polo de las células en la dirección que se desplaza es el anterior (apical) y el opuesto es el posterior (o antapical) (Fig. 14).

1.2.2. El dinocarion

En comparación con otros organismos, los dinoflagelados destacan por tener un núcleo de gran tamaño con características especiales que recibe su propio nombre: el dinocarion y su división se llama dinomitosis. Aunque en algunos géneros de aguas salobres (*Kryptoperidinium* y *Durinskia*) o marinos como *Podolampas* pueden encontrarse dos núcleos en la célula, uno es dinocarion y el otro es completamente eucariótico y procede de una microalga endocitobiótica (Schweiker y Elbrächter, 2004).

1.2.2.1. Ultraestructura

Los dinoflagelados son haplontes (células con una dotación cromosómica *n*). *Noctiluca* constituye una excepción, sus gametos son haploides y las células vegetativas son diploides (*2n*) (Zingmark, 1970; Soyer, 1972). Los contenidos de ácidos nucleicos por núcleo haploide oscilan entre los 3 picogramos de *Amphidinium carterae* a los 200 pgr de *Lingulodinium polyedra*. Otras algas eucariotas contienen entre 0,04 y 3 pgr de ADN, con un valor medio de 0,54 pgr por núcleo haploide (Spector, 1984). Cada pgr equivale aproximadamente a 1 Gb (10^9 pares de bases). Por ejemplo, el genoma humano con 3,2 Gb es aproximadamente unas cien veces menor que el genoma de un dinoflagelado.

No se ha secuenciado completamente el genoma de ningún dinoflagelado, aunque hay interés en especies con genomas más cortos como *Symbiodinium*, que facilitaría investigar fenómenos como el blanqueo del coral. Un genoma tan grande, no es esperable que contenga todos los genes únicos y funcionales. Los dinoflagelados tienen niveles superiores al 60% de secuencias repetidas. En las regiones 28S y 18S hay genes con secuencias no funcionales, mutados o pseudogenes, y aún se desconoce porque los dinoflagelados mantienen esos pseudogenes (Moreno *et al.*, 2005).

Los dinoflagelados tienen un número elevado de cromosomas por genoma haploide, entre 20-270, siendo menor en dinoflagelados parásitos (4-8) (Costas y Goyanes, 2005). En función del tipo de núcleo, los dinoflagelados se han subdividido en Dinokaryota y Syndinea. Syndinea tiene un núcleo eucariota más

convencional con cromosomas descondensados durante la división celular (interfase en el ciclo mitótico). Hay histonas presentes y a veces los centríolos (Chatton, 1920).

La mayor parte de los dinoflagelados entrarían dentro del grupo dinocariota, con el típico dinocarion al menos en una parte del ciclo de vida (en *Noctiluca* el dinocarion falta en estados del ciclo de vida; Soyer, 1972). El dinocarion se acerca a un núcleo eucariota, pero con algunos caracteres procariotas. A diferencia de células eucariotas, los dinocromosomas son fibrilares, permanentemente condensados y el huso mitótico es externo. El núcleo esta rodeado de una envoltura nuclear persistente y muy desarrollada en algunas especies. La dinomitosis es cerrada como ocurre en otros protistas y hongos, es decir, la envoltura nuclear no se rompe durante la división celular y faltan las histonas y nucleosomas.

El dinocarion se caracteriza por la falta de proteínas básicas llamadas histonas. Pequeñas cantidades de histonas están presentes en algunas especies dinocariontas, que no corresponden a las histonas eucariotas (Spector, 1984). A lo largo de la evolución los dinoflagelados perdieron las histonas de eucariotas y adquirieron genes para codificar proteínas básicas cercanas a las histonas a partir de genes de procariotas. El ADN tiene altos contenidos de guanina y citosina y más del 70% de bases raras o modificadas con una alta tasa de sustitución de timina por 5-hidroximetiluracil (HOMeU) (Rae, 1976). Sin histonas ni nucleosomas y con una relación proteína/ADN de 1:10 en lugar de 1:1 como el resto de eucariotas, es un enigma como los dinoflagelados consiguen empaquetar su ADN en una cromatina funcional.

El núcleo de los dinoflagelados se asemeja a las células eucariotas en la presencia de secuencias repetidas no codificantes de ADN en el genoma y presentan el ciclo celular eucariota. En los dinocromosomas falta el contacto directo con el huso extracelular. Estas características intermedias entre eucariotas y procariotas llevan a Dodge (1965) a proponer el término mesocariotas para definir a los dinoflagelados y proponer incluso su propio reino, pero más bien debe considerarse a los dinoflagelados como células eucariotas que han degenerado asemejándose en algunos aspectos a procariotas.

1.2.2.2. Bioluminiscencia

Asociada al núcleo de los dinoflagelados se encuentra la enzima luciferasa que en oscuridad e inducida por estimulación mecánica cataliza la oxidación de la luciferina (Hastings, 1989). A lo largo del día, el dinoflagelado sintetiza luciferina en unas vesículas llamadas corpúsculos centelleantes o 'scintillons' que migran del citoplasma al núcleo al final del día. La estimulación mecánica produce una reacción química y cambia el pH de 8 a 6 alrededor de los 'scintillons'. La luciferina se activa en estas condiciones ácidas y la luciferasa cataliza su oxidación, dando por resultado un destello de 0,1 a 0,5 segundos y un producto intermedio llamado oxiluciferina. La longitud de onda del destello corresponde al color azul, ~474-476 nm, que es el que menos se atenúa en el agua de mar, aunque *Lingulodinium* produce destellos rojos, 630-690 nm (Hastings, 1983). La bioluminiscencia es más intensa en *Noctiluca*, *Pyrocystis*, *Protoperidinium*, *Gonyaulax* y *Lingulodinium.* Los destellos por célula de *Pyrocystis noctiluca* y *P. fusiformis* son 1000 veces más intensos que para *Gonyaulax* y unas 100 veces más que *Ceratium fusus*, *Protoperidinium pentagonum* y *Pyrodinium bahamense* (Swift *et al.*, 1973). Los dinoflagelados son los únicos organismos del plancton con especies autótrofas capaces de producir bioluminiscencia. Sweeny (1963) considera que la mitad de las especies de dinoflagelados son bioluminiscentes. Dentro de una misma especie se pueden encontrar cepas luminiscentes y otras que carecen de esta propiedad, lo que ofrece dudas sobre la estricta necesidad de bioluminiscencia para su supervivencia.

1.2.3. Cloroplastos

Además de las especies heterótrofas (saprofíticas, parásitas, simbióticas, etc.) se estima que en torno al 50% de las especies de dinoflagelados tienen cloroplastos, pero son pocas las especies estrictamente fotótrofas. Muchos de los dinoflagelados autótrofos marinos son auxótrofos para varias vitaminas.

1.2.3.1. Ultraestructura y tipos de cloroplastos

Los cloroplastos están envueltos de una membrana triple, mientras que en otros protistas tienen dos o cuatro membranas, falta un retículo endoplásmico y los tilacoides se disponen en grupos de tres, como en euglenofitas.

Según estudios genéticos, los antecesores de los dinoflagelados no eran fotosintéticos y adquirieron los cloroplastos a lo largo de su evolución por endosimbiosis secundaria e incluso terciaria de una célula eucariota fotosintética

que adquirió a su vez el cloroplasto por endosimbiosis primaria (McFadden y Gilson, 1995). Eso genera una alta diversidad de plastos y pigmentos en dinoflagelados. Los principales son las clorofilas a y c, β-caroteno, xantofilas, peridinina, neoperidinina, dinoxantina, neodinoxantina y diatoxantina. El tipo de cloroplasto más común contiene el pigmento peridinina, usándose como marcador pigmentario válido para una gran parte de los dinoflagelados fotótrofos (Claustre, 1994). Se pueden encontrar otros tipos de plastos que pierden la peridinina y contienen clorofilas a+c y fucoxantina, derivado de una diatomea (*Kryptoperidinium* y *Durinskia*). También con clorofilas a+c con otro tipo de fucoxantina derivado de haptofícea por endosimbiosis terciaria como en *Karenia* y *Karlodinium*; clorofilas a+b, derivado de una clorofita como en *Gymnodinium chlorophorum* y *Lepidodinium viride* (probablemente originados de una prasinofícea); clorofilas a+c con ficobilina, derivado de una criptofícea (Schnepf y Elbrächter, 1999). La incorporación de cloroplastos de otras microalgas es un fenómeno que continua en dinoflagelados. Los *cleptocloroplastos* de *Dinophysis* derivan de criptofíceas o haptofíceas ingeridas y son temporalmente funcionales (Koike *et al.*, 2005). Otros Dinophysiales heterótrofos como *Histioneis*, *Citharistes* u *Ornithocercus* han modificado su morfología creando una gran cámara cingular extracelular, un *invernadero*, para albergar cianobacterias unicelulares con nitrogenasa responsables de la ficobilinas en este grupo (Foster *et al.*, 2006). En el caso de *Amphisolenia*, sin espacio en el collar cíngular, los cianobiontes son intracelulares (Norris, 1967).

La principal sustancia de reserva de los dinoflagelados son gránulos de almidón que se forman fuera de los cloroplastos. También pueden almacenar lípidos como el dinosterol y anfisterol que son casi exclusivos de dinoflagelados (presente en menor cantidad en diatomeas) (Boon *et al.*, 1979).

1.2.3.2 RuBisCO

La RuBisCO (Ribulosa-1,5-bisfosfato-carboxilasa) es la enzima más abundante en la tierra y es responsable de la fijación del carbono en la fotosíntesis. Mientras que la mayor parte de las microalgas tienen la típica RuBisCO aerobia, casi todos los dinoflagelados tienen la RuBisCO tipo II, una atípica forma que sólo se encuentra en bacterias anaeróbicas (Whitney *et al.*, 1995; Morse *et al.*, 1995). El genoma de los cloroplastos de plantas y algas consiste en 100-250 genes, normalmente codificados en ADN simple circular de un tamaño de 120-200 miles de pares de bases. Sin embargo, en dinoflagelados la mayor parte de los genes

de los cloroplastos, incluyendo el gen de la RuBisCO, se encuentran en el núcleo y sólo algunos genes están fuera del núcleo en forma de plásmidos como minicírculos (Zhang *et al.*, 1999). Algunos dinoflagelados que no tienen peridinina, tampoco tienen forma II de la RuBisCO, especulándose que evolutivamente pudiesen tener mismo origen.

Los dinoflagelados al albergar tanto especies autótrofas como heterótrofas se han clasificado bajo las reglas del Código Internacional de Nomenclatura Botánica para algas y plantas y bajo el Código Internacional de Nomenclatura Zoológica como protozoos y animales. Los paleontólogos decidieron por consenso en 1961 que los fósiles de dinoflagelados se regirían por el Código Botánico, sin embargo el consenso entre los investigadores de especies actuales no existe. En las últimas dos décadas los dinoflagelados suelen ser descritos bajo el Código Botánico (Greuter *et al.*, 2000). Por tanto, el término dinofíceas debería reemplazar al término dinoflagelado usado mucho antes por los zoólogos (Bütschli, 1885). Quizás la nomenclatura de los dinoflagelados debería estar regida por el Código de Protistas, pero ese código no existe.

1.2.4. Consecuencias ecológicas derivadas de su ultraestructura

Los estudios genéticos han situado a los dinoflagelados como células eucariotas en el grupo monofilético de los Alveolados, junto con los Apicomplexa y no lejos de los ciliados y foraminíferos. Los dinoflagelados, como su pariente cercano al agente causante de la malaria, tienen tendencia al parasitismo, simbiosis o heterotrofia, siendo la autotrofia una adquisición secundaria. Los dinoflagelados presentan una extraordinaria tendencia a incorporar los genes de otros organismos al genoma de su núcleo, siendo considerados como "*a remarkable evolutionary experiment*" (Hackett *et al.*, 2004). Una gran cantidad de genes les puede permitir sintetizar muchos compuestos, pero también un mayor gasto por mantener genes repetidos y en muchos casos no codificantes. Los genes de los cloroplastos están el núcleo y esto podría restar eficiencia al requerir una maquinaria biosintética para la ruta entre el núcleo y el cloroplasto. La baja tasa de crecimiento de dinoflagelados comparada con otros grupos se ha atribuido a la relación carbono-clorofila (Tang, 1996). Sin embargo, la peculiar ultraestructura de los dinoflagelados parece estar detrás de sus características fisiológicas y ecológicas. La RuBisCO tipo II de la mayor parte de los dinoflagelados es menos eficiente en diferenciar el CO_2 del O_2 que la forma I. A pesar de posibles mecanismos de concentración de carbono (Leggat *et al.*,

1999), una RuBisCO de origen anaerobio funcionando en ambiente aerobio resta eficiencia a la fotosíntesis comparada con otros grupos de fitoplancton como las diatomeas. La fotosíntesis es un fenómeno poco favorecido en dinoflagelados y eso explicaría la tendencia hacia otras formas de nutrición. La división mitótica en un núcleo tan grande es más lenta y costosa que en otros grupos de microalgas.

Los dinoflagelados tienen un gran genoma en forma de cristal líquido muy sensible a la turbulencia (Yeung y Wong, 2003; Wong y Kwok, 2005). La agitación no incide tanto en el crecimiento como en su división mitótica (Berdalet, 1992). Estas características podrían explicar la baja tasa de división de los dinoflagelados y también que sean muy sensibles a la turbulencia (Estrada *et al.*, 1987). Por tanto en las primeras etapas de la sucesión de especies fitoplanctónicas en aguas ricas en nutrientes y mayores niveles de turbulencia, los dinoflagelados fotosintéticos serían superados por la mayor tasa de división de las diatomeas.

La movilidad en las especies fotosintéticas permite regular su posición vertical optimizando los niveles lumínicos para la fotosíntesis e incluso mediante migraciones verticales pueden incorporar nutrientes de aguas profundas. La velocidad de ascenso-descenso parece incrementarse en formas coloniales como *Gymnodinium catenatum* (Fraga *et al.*, 1989). La suma de estos factores hace que los dinoflagelados sean más competitivos en aguas estratificadas frente a otros grupos de microalgas, predominando en mares tropicales o durante el verano en regiones templadas (Margalef, 1978).

2. Objetivos

Esta memoria de tesis tiene entre sus objetivos:

1. Cuantificar el número de especies de dinoflagelados libres marinos conocidos. Efectuar correcciones en su sinonimia, basadas en la bibliografía o en observaciones propias. Corregir errores en nomenclatura siguiendo el Código Internacional de Nomenclatura Botánica (Greuter *et al.*, 2000). Identificar aquellas especies o grupos de dinoflagelados de dudosa validez o escasamente conocidos, evaluando si el número de especies esta infra- o sobreestimado en cada grupo.
2. Cuantificar el número de especies basadas en la bibliografía en el Mar Mediterráneo y Mar Negro. Examinar las afinidades biogeográficas de esas especies con el objetivo de señalar las especies endémicas o de origen Indo-pacífico. Comparar los porcentajes de dinoflagelados endémicos e Indo-pacíficos con organismos macroscópicos. Discutir e identificar los problemas en el estudio de la biogeografía de dinoflagelados oceánicos.
3. Investigar la distribución y taxonomía de algunos grupos de dinoflagelados menos conocidos. Discutir sobre la variación morfológica en su ciclo de vida y la validez de las especies, así como su relación con otros grupos de dinoflagelados. Los grupos tratados son concretamente:
   - 3.1. Los dinoflagelados englobados en el orden Brachidiniales: *Asterodinium*, *Brachidinium* y *Microceratium*, evaluando su variabilidad intraespecífica, examinando su morfología y estableciendo sus relaciones con otros grupos.
   - 3.2. El género *Ceratoperidinium*: su variabilidad morfológica y las especies que lo componen.
   - 3.3. *Gynogonadinium* gen. prov. como ejemplo de un género de dinoflagelados muy distintivo, pero sin descripción previa.
   - 3.4. Noctilucales (excluyendo *Noctiluca*), grupo esencial en la evolución de los dinoflagelados del que se conoce poco sobre su distribución, se investigará la validez de especies descritas y su relación con otros dinoflagelados.
   - 3.5. En las Dinophysiales, se investiga la variabilidad morfológica descrita del género *Histioneis* como ejemplo de una excesiva descripción de nuevas especies en este orden.

3. Resultados (Artículos)

3.1. Diversidad y biogeografía:

3.1.1. ¿Cuántas especies?

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A list of free-living dinoflagellate species in the world's oceans

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A checklist of free-living marine dinoflagellates (Dinophyceae) is given. The nomenclature is brought up to date and synonyms are included. The spelling of several taxa is corrected according to the International Code of Botanical Nomenclature (ICBN). A total of 1555 species (117 genera) constitute the free-living marine dinoflagellates, with 135 new species in the period 1993 to 2003. The most numerous genera are: *Protoperidinium* (264 species), *Gymnodinium* (173 species), *Dinophysis+Phalacroma* (104+41 species), *Gyrodinium* (87 species), *Amphidinium* (76 species), Histioneis (65 species), *Ceratium* (64 species) and *Gonyaulax* (60 species).

Key words: Phytoplankton, checklist, Dinophyta, dinoflagellates, algae, nomenclature, taxonomy.

Introduction

Dinoflagellates constitute one of the main groups of marine protists. SCHILLER (1931–1937) provided a description of all the species, both marine and freshwater, known at that time. Later SOURNIA (1973, 1978, 1982, 1990, 1993) listed the new taxonomic entries published after SCHILLER (1931–1937). SOURNIA (1986) gave descriptions and illustrations of the marine genera of dinoflagellates, excluding information at the species level. After SCHILLER (1931–1937) no compilation of free-living marine dinoflagellates was made available. This study provides for the first time a checklist and evaluates the species richness of dinoflagellates in the world oceans.

Material and methods

This study is based on literature records of free-living dinoflagellates. The primary sources are SCHILLER (1931–1937) and SOURNIA (1973, 1978, 1982, 1990, 1993). References to new species and combinations published between 1993 and 2003 are provided in brackets in table 1. Species with their nomenclatural authorities and the date of the description are arranged alphabetically within the genus. Genera are ordered alphabetically within

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each family. SOURNIA (1973, 1978, 1982, 1990, 1993) reported lists of dinoflagellates in alphabetic order, with no classification. The present list does not pretend to propose any classification, but it is superior to a mere alphabetical list. The classification of the dinoflagellates is being continuously subjected to changes according to new findings, especially with the application of recent molecular techniques. This study follows the most common classification from the literature and is updated according to recent knowledge, but any classification is unavoidably associated with discrepancies among authors.

SOURNIA (1973, 1978, 1982, 1990, 1993) in his successive checklists of marine species did not report synonyms or doubtful species, except for the new combinations proposed. Sournia et al. (1991) reported 1424–1772 species (115–131 genera) of extant free-living marine dinoflagellates. The higher number included little known or doubtful species. The lower number according to SOURNIA et al. (1991) is »that of the taxa which look presently reliable and have a practical value to the taxonomist in charge of identifying a species«. However no list of reliable or doubtful species was reported. In this study, only taxa of very doubtful validity are marked with an asterisk (*) and not considered for species counting. However the number of taxa that should be considered doubtful is higher. Many taxa have not been reported in the last 80 years and the original descriptions are insufficient or inadequate. For example, when species of the genus *Dinophysis* are temporally maintained in cultures, several species turn out to be morphotypes in the life cycle of one taxon (e.g., REGUERA and GONZÁLEZ-GIL 2001). Thus, probably if the life cycles of species of genera such as *Histioneis* or *Amphisolenia* are investigated, the species number of these genera will be drastically reduced. On the other hand, many taxa such as gymnodiniacens remain un-described because they are considered to be co-specific and misidentified with known species. Taxa reported only from the identification of cysts have been excluded except when live cells have germinated from cysts.

Another difficulty is the separation of marine and freshwater species. Some freshwater species can tolerate marine conditions and in other cases the marine records are misidentifications. SOURNIA et al. (1991) reported that 240 species constitute continental dinoflagellates. The revisions by Sournia entitled »catalogue of marine dinoflagellates« included some freshwater species [for example *Prorocentrum playfairii*, SOURNIA (1990)]. GÓMEZ and BOICENCO (2004) provided a list of freshwater dinoflagellates found in the brackish waters of the Black Sea.

Results and discussion

The spelling of several taxa has been modified according to the International Code of Botanical Nomenclature (GREUTER et al. 2000). Although typographical and orthographical errors may be corrected, no change has been applied under the retention of original spelling provision of Article 60.1. For the species *Gambierdiscus belizeanus* Faust, *Ostreopsis caribbeana* Faust, *Plagiodinium belizeanum* Faust *et* Balech, *Prorocentrum belizeanum* Faust, *Protoperidinium belizeanum* Faust and *Prorocentrum caribbaeum* Faust and the orthographically correct epithets are »belizianum« and »caribaeum« respectively. The epithet »arabicum« is orthographically correct for *Prorocentrum arabianum* Morton *et* Faust.

For epithets commemorating persons, substantive epithets are more commonly applied than adjectival epithets. These cases are *Prorocentrum hoffmannianum* Faust instead of

»hoffmannii«; *Prorocentrum norrisianum* Faust instead of »norrisii« and *Prorocentrum ruetzlerianum* Faust instead of »ruetzleri«. No change was applied according to Article 60.1. (GREUTER et al. 2000).

Only a few epithets with the wrong gender termination (Art. 32.5) were modified to accord with Article 23.5.: *Prorocentrum panamense* Grzebyk, Sako *et* Berland [published as »panamensis«], *Prorocentrum tropicale* Faust [published as »tropicalis«], *Ostreopsis belizeana* Faust [published as »belizeanum«], *Ostreopsis caribbeana* Faust [published as »caribbeanus«] and *Ostreopsis marina* Faust [published as »marinus«], and the freshwater species *Peridinium belizense* Carty et Wujek [published as »belizensis«]. The genus *Takayama* de Salas, Bolch, Botes *et* Hallegraeff is named after Dr. Haruyoshi Takayama (male). In these cases is usual to add a Latin termination (i.e. Takayamaea). The epithet of the species *Akashiwo sanguinea* (Hirasaka) G.Hansen et Moestrup showed a feminine ending. The use of "Akashio" instead of "Akashiwo" is recommendable. No change is applied.

The epithet of *Gambierdiscus australis* Chinain *et* Faust is not a case of wrong gender termination. In the epithet that refers its geographical locality, Australes Islands (no Austral region), is lacking a suffix. It can be formed by adding Latin adjectival suffixes to the place-name such as –anus »australesanus« or –ensis »australesensis«. In addition, it is reported that the genus *Gaarderia* Carbonell-Moore is pre-ocupied by the extant coccolithophorid *Gaarderia* (Lecal) Kleijne.

Free-living marine dinoflagellates (excluding Phytodiniales Christensen ex Loeblich III) were represented by 1555 species (117 genera) (Tab. 1). The most numerous genera are: *Protoperidinium* (264 species), *Gymnodinium* (173 species), *Dinophysis+Phalacroma* (104+41 species), *Gyrodinium* (87 species), *Amphidinium* (76 species), Histioneis (65 species), *Ceratium* (64 species) and *Gonyaulax* (60 species). In the last decade, since the last revision by SOURNIA (1993), 135 new species (no combinations) have been described (excluding several new extant species, known only from the fossil record). The new entries mainly belong to the genera *Gymnodinium* (+*Karenia*) (19+6 species), *Prorocentrum* (19 species), *Lissodinium* (17 species), *Amphidiniopsis* (8 species), *Gyrodinium* (+*Takayama*) (8+5 species) and *Heterocapsa* (6 species). The genera *Akashiwo*, *Amphidiniella*, *Bysmatrum*, *Gaarderia*, *Heterobractum*, *Karenia*, *Karlodinium*, *Lessardia*, *Mysticella*, *Plagiodinium*, *Polarella* and *Takayama* have been erected in the period 1993 to 2003.

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Tab. 1. List of free-living marine dinoflagellates. Species names following the International Code of Botanical Nomenclature (ICBN; GREUTER et al. 2000). References of the new species and combinations published between 1993 and 2003 are provided. * – Taxa of doubtful validity

DINOPHYCEAE G.S. West *et* Fritsch 1927

Actiniscales Sournia 1984

Actiniscaceae Kützing 1844

1 *Achradina* Lohmann 1902

1 *Achradina pulchra* Lohmann 1902 (=*A. pulchra* f. *angusta* (Lohmann) Nival 1969, f. *reticulata* (Lohmann) Nival 1969, f. *angusta* (Lohmann) Nival 1969)

2 *Actiniscus* Ehrenberg 1843

2 *Actiniscus pentasterias* (Ehrenberg 1840) Ehrenberg 1854 (=*Dictyocha pentasterias* Ehrenberg 1840, *Gymnaster striatum* Meunier 1910, *G. helix* Meunier 1910, *G. pentasterias* Schütt 1895)

3 *Amphilothus* Schütt 1895

3 *Amphilothus elegans* (Schütt 1895) Kofoid 1907

4 *Amphilothus quincuncialis* Kofoid 1907

4 *Dicroerisma* F.J.R. Taylor *et* Cattell 1969

5 *Dicroerisma psilonereiella* F.J.R. Taylor *et* Cattell 1969

Brachidiniales Loeblich III *ex* Sournia 1984

Brachidiniaceae Sournia 1972 [the criteria for the differentiation of species require further research, related to Gymnodiniales Lemmermann]

5 *Asterodinium* Sournia 1972

6 *Asterodinium gracile* Sournia 1972

7 *Asterodinium libanum* Abboud-Abi Saab 1989 [probably a morphotype of the type species]

8 *Asterodinium spinosum* Sournia 1972 [probably a morphotype of the type species]

6 *Brachidinium* F.J.R. Taylor 1963 [usually as *Brachydinium*, see Gómez (2003)]

9 *Brachidinium brevipes* Sournia 1972 [probably a morphotype of the type species]

10 *Brachidinium capitatum* F.J.R. Taylor 1963

**Brachidinium catenatum* F.J.R. Taylor 1967

11 *Brachidinium taylorii* Sournia 1972 [probably a morphotype of the type species]

Tab. 1. – continued

Dinophysiales Lindemann 1928

Citharistaceae Kofoid *et* Skogsberg 1928

7 ***Citharistes*** Stein 1883
12 *Citharistes apsteinii* Schütt 1895
13 *Citharistes regius* Stein 1883

Dinophysaceae Stein 1883

8 ***Amphisolenia*** Stein 1883 (32 species)
14 *Amphisolenia astragalus* Kofoid *et* Michener 1911
15 *Amphisolenia asymmetrica* Kofoid 1907
16 *Amphisolenia bidentata* Schröder 1900 (non *A. bidentata* Pavillard 1916, non *A. bidentata* Okamura 1907)
17 *Amphisolenia bifurcata* Murray *et* Whitting 1899 (=*A. thrinax* Zacharias 1906, *A. projecta* Kofoid 1907)
18 *Amphisolenia biprojecta* Saifullah *et* Hassan 1973
19 *Amphisolenia bispinosa* Kofoid 1907
20 *Amphisolenia brevicauda* Kofoid 1907
21 *Amphisolenia clavipes* Kofoid 1907
22 *Amphisolenia complanata* Kofoid *et* Skogsberg 1928
23 *Amphisolenia curvata* Kofoid 1907
**Amphisolenia elegans* Böhm 1933
24 *Amphisolenia elongata* Kofoid *et* Skogsberg 1928
25 *Amphisolenia extensa* Kofoid 1907
26 *Amphisolenia globifera* Stein 1883 (=*A. globosa* Gran 1912, *A. tenella* Gran 1912)
27 *Amphisolenia inflata* Murray *et* Whitting 1899
28 *Amphisolenia laticincta* Kofoid 1907
29 *Amphisolenia lemmermannii* Kofoid 1907
30 *Amphisolenia microcephalus* Abé 1967
31 *Amphisolenia mozambica* Sournia 1967 (=?*A. sigma* Halim 1965)
32 *Amphisolenia palaeotheroides* Kofoid 1907
33 *Amphisolenia palmata* Stein 1883 (=*A. bidentata* Pavillard 1916 partim)

Tab. 1. – continued

34 *Amphisolenia quadricauda* Kofoid *et* Michener 1911 (=*A. quinquecauda* Kofoid 1907)
35 *Amphisolenia quadrispina* Kofoid 1907
37 *Amphisolenia rectangulata* Kofoid 1907
38 *Amphisolenia schauinslandii* Lemmermann 1899
39 *Amphisolenia schroederi* Kofoid 1907
40 *Amphisolenia sigma* Halim 1965 (=?*A. spinulosa* Kofoid 1907,?*A. mozambica* Sournia 1967)
41 *Amphisolenia spinulosa* Kofoid 1907
42 *Amphisolenia taylorii* Saifullah *et* Hassan 1973
43 *Amphisolenia testa* Balech 1962
44 *Amphisolenia thrinax* Schütt 1893 (non *A. thrinax* Zacharias 1906)
45 *Amphisolenia truncata* Kofoid *et* Michener 1911
9 ***Dinofurcula*** Kofoid *et* Skogsberg 1928 (=***Phalacroma*** Stein 1883 partim)
46 *Dinofurcula ultima* (Kofoid 1906) Kofoid *et* Skogsberg 1928
47 *Dinofurcula ventralis* Kofoid *et* Skogsberg 1928
10 ***Dinophysis*** Ehrenberg 1839 (=***Phalacroma*** Stein 1883 partim) (104 species) [see *Phalacroma*]
48 *Dinophysis acuminata* Claparède *et* Lachmann 1859 (=*D. ovum* var. *baltica* Paulsen 1908, *D. arctica* sensu Woloszyńska 1928, *D. baltica* (Paulsen) Woloszyńska 1928, *D. baltica* (Paulsen) Kofoid *et* Skogsberg 1928, *D. cassubica* Woloszyńska 1928, *D. levanderi* Woloszyńska 1928, *D. paulsenii* Woloszyńska 1928, *D. boehmii* Paulsen 1949 *ex* Balech 1971, *D. borealis* Paulsen 1949, *D. lachmannii* Paulsen 1949)
49 *Dinophysis acuta* Ehrenberg 1839 (=*D. dens* Pavillard 1915, *D. groenlandica* (Schiller 1933) Balech 1967)
50 *Dinophysis acutissima* Gaarder 1954
51 *Dinophysis alata* Jørgensen 1923 (=?*D. alata* Böhm 1931, non *D. alata* (Wood 1954) Balech 1967)
52 *Dinophysis amandula* (Balech 1967) Sournia 1973 (=*D. amygdala* Balech 1967, *Ph. ovum* Schütt 1895, non *D. amygdalus* Paulsen 1949, non *D. ovum* Schütt 1895)
53 *Dinophysis amphora* Balech 1971
54 *Dinophysis anabilis* Abé 1967
55 *Dinophysis apiculata* Meunier 1910
56 *Dinophysis arctica* Mereschkowsky 1879 (=*D. laevis* (Bergh 1881) Pouchet 1883, *D. rotundata* Levander 1894, *D. granulata* Cleve 1899, non *D. laevis* Bergh, non *D. rotundata* Claparède *et* Lachmann 1859, non *D. arctica* sensu Woloszyńska 1928,?*D. vertex* Meunier 1910)

Tab. 1. – continued

57 *Dinophysis balechii* Norris *et* Berner 1970
58 *Dinophysis bibulbus* Balech 1971
**Dinophysis biceras* Schiller 1928 (=*Dinoceras biceras* Schiller 1933)
59 *Dinophysis braarudii* (Nordli 1951) Balech 1967 (=*Ph. braarudii* Nordli)
60 *Dinophysis brevisulcus* Tai *et* Skogsberg 1934
61 *Dinophysis capitulata* Balech 1967
62 *Dinophysis carpentariae* Wood 1963
63 *Dinophysis caudata* Saville-Kent 1881 (=*D. homunculus* Stein 1883; related to *D. tripos* Gourret 1883)
**Dinophysis collaris* Kofoid *et* Skogsberg 1928
64 *Dinophysis cornuta* (Peters 1928) Balech 1967 (=*Ph. cornutum* Peters)
**Dinophysis crassior* Paulsen 1949 (=*D. norvegica* var. *crassior* Paulsen 1907, small cell of *D. norvegica* Claparède *et* Lachmann)
65 *Dinophysis curvata* Schiller 1933 (=*D. sphaerica* Stein 1883 partim, non *D. diegensis* var. *curvata* Kofoid 1907)
66 *Dinophysis cyrtoptera* Balech 1978
**Dinophysis dens* Pavillard 1915 (small cell of *D. acuta* Ehrenberg)
67 *Dinophysis dentata* Schiller 1928
**Dinophysis diegensis* Kofoid 1907 (small cell of *D. caudata* Saville-Kent 1881)
**Dinophysis diegensis* var. *curvata* Kofoid 1907 (small cell of *D. tripos* Gourret)
68 *Dinophysis dolychopterygium* (Murray *et* Whitting 1899) Balech 1967
69 *Dinophysis doryphorum* (Stein 1883) Abé *vel* Balech 1967 (=*D. doryphorides* (P. Dangeard 1927) Balech 1967)
70 *Dinophysis dubia* Balech 1978
71 *Dinophysis ellipsoides* Kofoid 1907 [related to *D. acuminata*]
72 *Dinophysis equalantii* Balech 1971
73 *Dinophysis exigua* Kofoid *et* Skogsberg 1928
74 *Dinophysis fortii* Pavillard 1923 (=*D. laevis* Pouchet 1883, *D. ovum* Schütt sensu Martin 1929, *D. lapidistrigiliformis* Abé 1967, *D. intermedia* Pavillard 1916, non *D. internedia* Cleve 1900)
75 *Dinophysis fortunata* Sournia 1973 (=*Ph. longialatum* Gaarder 1954, *Heteroschisma longialata* (Gaarder) Balech 1967, non *D. longialata* Gran *et* Braarud 1935)
76 *Dinophysis gaarderae* Sournia 1973 (=*Ph. robustum* Gaarder 1954, non *D. robusta* Gran *et* Braarud 1935)

Tab. 1. – continued

77 *Dinophysis granii* Paulsen 1949
78 *Dinophysis hasleae* Balech 1973
79 *Dinophysis hastata* Stein 1883 (=*D. uracantha* (Stein) E.S. Silva 1956)
80 *Dinophysis hyalina* Wood 1963
81 *Dinophysis intermedia* Cleve 1900 (non *D. intermedia* Pavillard 1916)
82 *Dinophysis irregularis* (Lebour 1925) Balech 1967 (=*Ph. irregulare* Lebour)
**Dinophysis islandica* Paulsen 1949
**Dinophysis joergersenii* Kofoid *et* Skogsberg 1928 (=*D. triacantha* Jørgensen 1923 partim)
83 *Dinophysis lacrima* (Gaarder 1954) Balech 1967 (=?*D. elongatum* (Jørgensen 1923) Abé *vel* Balech 1967)
84 *Dinophysis laevis* Claparède *et* Lachmann 1859 (non *D. laevis* Bergh 1881, non *D. laevis* Pouchet 1883)
**Dinophysis lapidistrigilliformis* Abé 1967 (small cell of *D. fortii* Pavillard 1923)
85 *Dinophysis lata* (Gaarder 1954) Balech 1967 (=*Ph. latum* Gaarder, non *D. lata* Balech 1971=*D. sourniai* Balech 1978)
86 *Dinophysis laticincta* Balech 1979
**Dinophysis longialata* Gran *et* Braarud 1935
87 *Dinophysis meteorii* Böhm 1933
88 *Dinophysis minuta* (Cleve 1900) Balech 1967 (=*D. elongata* (Jørgensen 1923) Abé *vel* Balech 1967)
89 *Dinophysis meunieri* Schiller 1928 (=*D. cuneiformis* Meunier 1910, non *D. cuneiformis* Mangin 1922)
90 *Dinophysis michaeli* Sournia 1973 (=*Ph. limbatum* Kofoid *et* Michener 1911)
91 *Dinophysis micropleura* Balech 1971
92 *Dinophysis micropterygia* P. Dangeard 1927
93 *Dinophysis microstrigilliformis* Abé 1967
94 *Dinophysis miles* Cleve 1900 (=*Heteroceras schroeteri* Forti 1901)
95 *Dinophysis nitroides* Sournia 1973 (=*Ph. okamurai* Pavillard 1931, non *D. okamurai* Kofoid *et* Skogsberg 1928)
96 *Dinophysis modesta* (Böhm 1936) Balech 1967 (=*Ph. modestum* Böhm)
97 *Dinophysis monacantha* Kofoid *et* Skogsberg 1928 (non *Ph. monacanthum* Gail 1950)
98 *Dinophysis moresbyensis* Wood 1963
99 *Dinophysis mucronata* (Kofoid *et* Skogsberg 1928) Sournia 1973 (=*D. paulsenii* (Schiller 1928) Balech 1967, non *D. paulsenii* Woloszyńska 1928)
100 *Dinophysis neolenticula* Sournia 1973 (=*Ph. lenticulata* Kofoid 1907, non *D. lenticula* Daday 1888, nec *D. lenticula* Pavillard 1916)

Tab. 1. – continued

101 *Dinophysis nias* Karsten 1907 (=*D. triacantha* Karsten 1907)
102 *Dinophysis norvegica* Claparède *et* Lachmann 1859 (=*D. norvegica* var. *debilior* Paulsen 1907, *D. debilior* (Paulsen) Paulsen 1949)
103 *Dinophysis okamurai* Kofoid *et* Skogsberg 1928 (=*D. vanhoffenii* Okamura 1907 partim, non *D. vanhoffenii* Ostenfeld 1899)
104 *Dinophysis odiosa* (Pavillard 1930) Tai *et* Skogsberg 1934 (=*Ph. odiosum* Pavillard 1930, *Ph. hastatum* Pavillard 1909)
105 *Dinophysis operculata* (Stein 1883) Balech 1967
106 *Dinophysis opposita* Wood 1963
107 *Dinophysis oviformis* Chen *et* Ni 1988 (non *D. oviformis* Schiller 1928)
108 *Dinophysis ovum* Schütt 1895 (=*D. brevisulcus* Tai *et* Skogsberg 1937 partim, *D. antarctica* Balech 1958, non *Ph. ovum* Schütt 1895)
109 *Dinophysis pacifica* Wood 1963
110 *Dinophysis paralata* Sournia 1973 (=*D. alata* (Wood 1954) Balech 1967)
111 *Dinophysis parva* Schiller 1928 (=*D. infundibulus* Schiller 1928)
112 *Dinophysis perforata* Sournia 1973 (=*D. porosa* (Kofoid *et* Skogsberg 1928) Balech 1967)
113 *Dinophysis planiceps* (Schiller 1928) Balech 1967 (=*Ph. planiceps* Schiller)
114 *Dinophysis porodictyum* (Stein 1883) Abé *vel* Balech 1967 (=*D. amygdala* Balech 1971, non *D. amygdala* 1967)
115 *Dinophysis punctata* Jørgensen 1923 (non *D. punctata* Balech 1971)
116 *Dinophysis pusilla* Jørgensen 1923
117 *Dinophysis recurva* Kofoid *et* Skogsberg 1928 (=*D. lenticula* Pavillard 1916, non Daday 1888)
118 *Dinophysis rete* Sournia 1973 (=*D. reticulata* (Kofoid 1907) Balech 1967, non *D. reticulata* Gaarder 1954)
119 *Dinophysis reticulata* Gaarder 1954 (non *D. reticulata* (Kofoid 1907) Balech 1967)
120 *Dinophysis richardii* (Pavillard 1934) Balech 1967
**Dinophysis robusta* Gran *et* Braarud 1935
121 *Dinophysis rudgei* Murray *et* Whitting 1899 (non *Ph. rudgei* Murray *et* Whitting 1899)
122 *Dinophysis rugosa* Kofoid *et* Michener 1911 (=*Histiophysis rugosa* Kofoid *et* Michener 1911)
123 *Dinophysis ruudii* (Braarud 1935) Balech 1967 (=*Ph. ruudii* Braarud)
124 *Dinophysis sacculus* Stein 1883 (=*D. acuminata* f. *reniformis* Pavillard 1905, *D. acuminata* f. *reniformis* (Pavillard 1905) Zingone, Montresor *et* Marino 1998, *D. pavillardii* Schröder 1906, *D. reniformis* (Pavillard) Kofoid *et* Skogsberg 1928, *D. ventrecta* Schiller 1933, *D. phaseolus* E.S. Silva 1952) [Zingone *et al.* (1998)]
125 *Dinophysis scabra* Sournia 1973 (=*Ph. rugosum* Gaarder 1954)
126 *Dinophysis schilleri* Sournia 1973 (=*Ph. sphaeroideum* Schiller 1928)

Tab. 1. – continued

127 *Dinophysis schroederi* Pavillard 1909
128 *Dinophysis schuettii* Murray *et* Whitting 1899 (=*D. uracantha* Schütt 1895, non *D. uracantha* Stein 1883)
129 *Dinophysis scrobiculata* Balech 1971 (=*Ph. scrobiculata* (Balech) Díaz-Ramos *et* Estrella *in* Díaz-Ramos 2000) [Díaz-Ramos (2000)]
130 *Dinophysis semen* Meunier 1910
131 *Dinophysis siankanensis* Becerril-Almazán *et* Hernández-Becerril 2002 [Becerril-Almazán and Hernández-Becerril (2002)]
132 *Dinophysis similis* Kofoid *et* Skogsberg 1928 (=*D. sphaerica* Schütt 1895, *D. simplex* Balech 1962=*D. tai Balech* 1971, non *D. simplex* Böhm 1933)
133 *Dinophysis simplex* Böhm 1933 (non *D. simplex* Balech 1962=*D. tai* Balech 1971=*D. similis* Kofoid *et* Skogsberg 1928)
**Dinophysis skagii* Paulsen 1949 (small cell of *D. acuminata*)
134 *Dinophysis sourniai* Balech 1978 (=*D. lata* Balech 1971, non *D. lata* (Gaarder 1954) Balech 1967)
135 *Dinophysis sphaerica* Stein 1883 (=*D. vanhoffenii* Ostenfeld 1899, non *D. sphaerica* Schütt 1895)
136 *Dinophysis spinata* (Peters 1928) Balech 1967
**Dinophysis spinosa* Rampi 1950
137 *Dinophysis subcircularis* Paulsen 1949
138 *Dinophysis swezyae* Kofoid *et* Skogsberg 1928
139 *Dinophysis symmetrica* (Gaarder 1954) Balech 1967
140 *Dinophysis tailisunii* Chen *et* Ni 1988
**Dinophysis taylorii* Hernández-Becerril 1992 (small cell of *D. tripos*/*D. caudata*)
141 *Dinophysis tenuivelata* Balech 1973
142 *Dinophysis thompsonii* (Wood 1954) Balech 1967
**Dinophysis trapezium* Kofoid *et* Skogsberg 1928
**Dinophysis triacantha* Kofoid 1907 (non *D. triacantha* Karsten 1907)
143 *Dinophysis tripos* Gourret 1883 (=*D. caudata* var. *tripos* (Gourret) Gail 1950)
144 *Dinophysis truncata* Cleve 1901 (=*D. cuneiformis* Mangin 1922, non *D. cuneiformis* Meunier 1910)
145 *Dinophysis tuberculata* Mangin 1926 (=*D. carinata* Peters 1928)
146 *Dinophysis turbinea* (Kofoid *et* Michener 1911) Balech 1967
147 *Dinophysis umbosa* Schiller 1928
148 *Dinophysis uracantha* Stein 1883 (non *D. uracantha* Schütt 1895=*D. schuettii* Murray *et* Whitting 1899)
149 *Dinophysis urceola* Kofoid *et* Skogsberg 1928

Tab. 1. – continued

150 *Dinophysis vertex* Meunier 1910 (=?*D. arctica* Mereschkowsky 1879)
151 *Dinophysis whiteleggei* (Wood 1954) Balech 1967
11 Heteroschisma Kofoid *et* Skogsberg 1928
152 *Heteroschisma globulus* Schiller 1933 (=*Phalacroma globulus* Schütt 1895)
153 *Heteroschisma pirum* (Gaarder 1954) Balech 1967 (=*Phalacroma pirum* Gaarder)
154 *Heteroschisma inaequale* Kofoid *et* Skogsberg 1928 (=*Latifascia inaequale* (Kofoid *et* Skogsberg) Loeblich Jr. *et* Loeblich III 1966)
155 *Heteroschisma subantarcticum* Balech 1971
12 *Histioneis* Stein 1883 (=***Parahistioneis*** Kofoid *et* Skogsberg 1928) (65 species)
156 *Parahistioneis acutiformis* Rampi 1947 (=?*H. diamantinae* Wood 1963)
157 *Histioneis aequatorialis* Wood 1963
158 *Histioneis australiae* Wood 1963 (=?*H. moresbyensis* Wood 1963)
159 *Histioneis biremis* Stein 1883
160 *Histioneis bougainvillae* Wood 1963
161 *Histioneis caminus* Böhm 1931 *in* Schiller 1933
162 *Histioneis carinata* Kofoid 1907
163 *Histioneis cerasus* Böhm 1931 *in* Schiller 1933
164 *Histioneis cleaveri* Rampi 1952
165 *Histioneis costata* Kofoid *et* Michener 1911 (=?*H. elongata* Kofoid *et* Michener 1911)
166 *Histioneis crateriformis* Stein 1883 (=*H. reticulata* Kofoid 1907)
167 *Histioneis cymbalaria* Stein 1883 (=*H. skogsbergii* Schiller 1933, *H. depressa* Schiller 1933, *H. speciosa* Rampi 1969)
168 *Histioneis dentata* Murray *et* Whitting 1899
169 *Histioneis detonii* Rampi 1947 (=?*H. cleaveri* Rampi 1952)
170 *Histioneis diamantinae* Wood 1963 (=?*P. acutiformis* Rampi 1947)
171 *Histioneis diomedeae* Kofoid *et* Michener 1911 (=*P. diomedeae* (Kofoid *et* Michener) Kofoid *et* Skogsberg 1928)
172 *Histioneis dubia* Böhm 1933 (=?*H. mediterranea* sec Rampi)
173 *Histioneis elongata* Kofoid *et* Michener 1911 (=*H. subcarinata* Rampi 1947,?*H. costata* Kofoid *et* Michener 1911)
174 *Histioneis fragilis* Böhm 1931 *in* Schiller 1933 (=?immature *H. milneri* Murray *et* Whitting 1899)
175 *Histioneis garrettii* Kofoid 1907 (=*P. garrettii* (Kofoid) Kofoid *et* Skogsberg 1928)

Tab. 1. – continued

176 *Parahistioneis gascoynensis* Wood 1963
177 *Histioneis gregoryi* Böhm 1936 (=*?H. pachypus* Böhm 1931 *in* Schiller 1933)
178 *Histioneis gubernans* Schütt 1895 (=*H. expansa* Rampi 1947, *H. ligustica* Rampi 1940)
179 *Histioneis highleyi* Murray *et* Whitting 1899
180 *Histioneis hyalina* Kofoid *et* Michener 1911 (=*?H. longicollis* Kofoid 1907)
181 *Histioneis imbricata* Halim 1960 (=*?H. longicollis* Kofoid 1907)
182 *Histioneis inclinata* Kofoid *et* Michener 1911 (=*H. alata* Rampi 1947)
183 *Histioneis inornata* Kofoid *et* Michener 1911
184 *Histioneis isselii* Forti 1932 (=*?H. elongata* sec Böhm 1936)
185 *Histioneis joergensenii* Schiller 1928 (=*?H. vouckii* Schiller 1928,=*?H. planeta* Wood 1963)
186 *Histioneis josephinae* Kofoid 1907 (=*?H. megalocopa* Stein 1883)
187 *Histioneis karstenii* Kofoid *et* Michener 1911 (=*P. karstenii* (Kofoid *et* Michener) Kofoid *et* Skogsberg 1928)
188 *Histioneis lanceolata* Wood 1963
189 *Histioneis longicollis* Kofoid 1907 (=*H. elegans* Halim 1960, *H. faouzii* Halim 1960, *H. kofoidii* Forti *et* Issel 1925, *H. minuscula* Rampi 1950, *H. sublongicollis* Halim 1960, *H. villafranca* Halim 1960)
190 *Histioneis marchesonii* Rampi 1941
191 *Histioneis mediterranea* Schiller 1928 (=*?H. reticulata* Kofoid 1907)
192 *Histioneis megalocopa* Stein 1883 (=*H. dolon* Murray *et* Whitting 1899)
193 *Histioneis milneri* Murray *et* Whitting 1899 (=*H. helenae* Murray *et* Whitting 1899, *H. hippoperoides* Kofoid *et* Michener 1911)
194 *Histioneis mitchellana* Murray *et* Whitting 1899 (=*H. mitchelliana* Schröder 1906,*?H. pulchra* Kofoid 1907)
195 *Histioneis moresbyensis* Wood 1963 (=*?H. costata* Kofoid *et* Michener 1911)
196 *Histioneis navicula* Kofoid 1907 (=*?H. oceanica* Rampi 1950)
197 *Histioneis oceanica* Rampi 1950 (=*?H. navicula* Kofoid 1907)
198 *Histioneis oxypteris* Schiller 1928 (=*?H. paulsenii* Kofoid 1907)
199 *Parahistioneis pachypus* Böhm 1931 *in* Schiller 1933 (=*P. varians* Böhm 1933,=*?H. gregoryi* Böhm 1936)
200 *Histioneis pacifica* Kofoid *et* Skogsberg 1928 (=*H. pavillardii* Rampi 1939, *H. bernhardii* Rampi 1969)
201 *Histioneis panaria* Kofoid *et* Skogsberg 1928 (=*?H. panda* Kofoid *et* Michener 1911)
202 *Histioneis panda* Kofoid *et* Michener 1911 (=*!H. panaria* Kofoid *et* Skogsberg 1928)
203 *Histioneis para* Murray *et* Whitting 1899 (=*P. conica* Böhm 1931 *in* Schiller 1933)

Tab. 1. – continued

204 *Histioneis paraformis* (Kofoid *et* Skogsberg 1928) Balech 1971 (=*H. para* Okamura 1912, *P. acuta* Böhm 1931 *in* Schiller 1933)
205 *Histioneis paulsenii* Kofoid 1907 (=?*H. crateriformis* Stein 1883,?*H. reticulata* Kofoid 1907 sec Balech 1988)
206 *Parahistioneis pieltainii* Osorio-Tafall 1942 (=?*H. sphaeroidea* Rampi 1947,?*H. tubifera* Böhm 1931 *in* Schiller 1933)
207 *Histioneis pietschmannii* Böhm 1931 *in* Schiller 1933
208 *Histioneis planeta* Wood 1963 (=?*H. longicollis* Kofoid 1907)
209 *Histioneis pulchra* Kofoid 1907 (=?*H. mitchellana* Murray *et* Whitting 1899)
210 *Histioneis rampii* Halim 1960 (=?*H. cymbalaria* Stein 1883)
211 *Histioneis reginella* Kofoid *et* Michener 1911
212 *Histioneis remora* Stein 1883 (=?*H. sphaeroidea* Rampi 1947)
213 *Histioneis robusta* Rampi 1969
214 *Histioneis rotundata* Kofoid *et* Michener 1911 (=*P. rotundata* (Kofoid *et* Michener) Kofoid *et* Skogsberg 1928)
215 *Histioneis schilleri* Böhm 1931 *in* Schiller 1933
216 *Histioneis simplex* Wood 1963
217 *Parahistioneis sphaeroidea* Rampi 1947 (=?*H. pieltainii* Osorio-Tafall 1942,=?*H. tubifera* Böhm 1931 *in* Schiller 1933)
218 *Histioneis striata* Kofoid *et* Michener 1911 (=*H. variabilis* Schiller 1933, *H. steinii* Schiller 1928, *H. parallela* Gaarder 1954)
219 *Histioneis tubifera* Böhm 1931 *in* Schiller 1933 (=?*H. pieltainii* Osorio-Tafall 1942,=?*H. sphaeroidea* Rampi 1947)
220 *Histioneis vouckii* Schiller 1928 (=?*H. joergensenii* Schiller 1928)
Metadinophysis Nie *et* Wang 1941 (=?***Dinophysis*** Ehrenberg 1839)
**Metadinophysis sinensis* Nie *et* Wang 1941
13 ***Metaphalacroma*** Tai *et* Skogsberg 1934
221 *Metaphalacroma skogsbergii* Tai *in* Tai *et* Skogsberg 1934
14 ***Ornithocercus*** Stein 1883 (15 species)
222 *Ornithocercus australis* Wood 1963
223 *Ornithocercus bilobatus* Rampi 1950 (=?*O. quadratus* f. *intermedia* Kofoid *et* Skogsberg 1928)
224 *Ornithocercus carpentariae* Wood 1963
225 *Ornithocercus cristatus* Matzenauer 1933
226 *Ornithocercus francescae* (Murray 1899) Balech 1962 (=*O. carolinae* Kofoid 1907, *Histioneis francescae* Murray *in* Murray *et* Whitting 1899)
227 *Ornithocercus formosus* Kofoid *et* Michener 1911

Tab. 1. – continued

228 *Ornithocercus geniculatus* P. Dangeard 1927
229 *Ornithocercus heteroporoides* Abé 1967
230 *Ornithocercus heteroporus* Kofoid 1907 (=*O. biclavatus* Wood 1954, *O. triclavatus* Wood 1954)
231 *Ornithocercus magnificus* Stein 1883 (=*O. minor* Jørgensen 1923, non *O. magnificus* Bütschli 1885)
232 *Ornithocercus quadratus* Schütt 1900 (=*O. assimilis* Jørgensen 1923, *Histioneis quadrata* Lemmermann 1901, *O. galea* (Pouchet 1883) Abé 1967)
233 *Ornithocercus skogsbergii* Abé 1967
234 *Ornithocercus splendidus* Schütt 1895 (=*Histioneis splendida* Murray *et* Whitting 1899)
235 *Ornithocercus steinii* Schütt 1900 (=*O. serratus* Kofoid 1907, *O. orbiculatus* Kofoid *et* Michener 1911)
236 *Ornithocercus thumii* (Schmidt 1888) Kofoid *et* Skogsberg 1928
15 *Phalacroma* Stein 1883 (=***Dinophysis*** Ehrenberg 1839 partim) (41 species) [*Phalacroma* has been considered a synonym of *Dinophysis* but the genus is maintained on the basis of the larger height of the epitheca and the prevailing heterotrophic behaviour. This is still a matter of debate]
237 *Phalacroma acutum* (Schütt 1895) Pavillard 1916 (=*D. acutoides* Balech 1967, non *D. acuta* Ehrenberg 1839)
238 *Phalacroma apicatum* Kofoid *et* Skogsberg 1928 (=*D. apicata* (Kofoid *et* Skogsberg) Abé *vel* Balech 1967)
239 *Phalacroma argus* Stein 1883 (=*D. argus* (Stein) Abé *vel* Balech 1967)
240 *Phalacroma biceps* (Schiller 1928) Schiller 1933 (=*D. biceps* Schiller)
241 *Phalacroma bipartitum* Kofoid *et* Skogsberg 1928 (=*D. bipartita* (Kofoid *et* Skogsberg) Balech 1967)
242 *Phalacroma circumcinctum* Kofoid *et* Michener 1911 (=*D. circumcincta* (Kofoid *et* Michener) Balech 1967)
243 *Phalacroma circumsutum* Karsten 1907 (=*D. circumsutum* (Karsten) Balech 1967)
244 *Phalacroma complanatum* Gaarder 1954
245 *Phalacroma contractum* Kofoid *et* Skogsberg 1928 (=*D. contracta* (Kofoid *et* Skogsberg 1928) Balech 1967, *Ph. ruudii* Braarud 1935)
246 *Phalacroma cuneolus* Kofoid *et* Skogsberg 1928 (=*D. cuneolus* (Kofoid *et* Skogsberg) Balech 1967)
247 *Phalacroma cuneus* Schütt 1895 (=*D. cuneus* (Schütt) Abé *vel* Balech 1967, *Ph. blackmanii* Murray *et* Whitting 1899, *Ph. triangulare* Wood 1954, *Dinophysis triangulare* (Wood) Balech 1967)
248 *Phalacroma doryphorum* Stein 1883
249 *Phalacroma expulsum* (Kofoid *et* Michener 1911) Kofoid *et* Skogsberg 1928 (=*P. stenopterygium* Jørgensen 1923)
250 *Phalacroma favus* Kofoid *et* Michener 1911 (=*P. hindmarchii* Pavillard 1916)
251 *Phalacroma fimbriatum* Kofoid *et* Michener 1911 (=*D. fimbriata* (Kofoid *et* Michener) Balech 1967)
252 *Phalacroma giganteum* Kofoid *et* Michener 1911 (=*D. gigantea* (Kofoid *et* Michener) Balech 1967)

Tab. 1. – continued

253 *Phalacroma globulus* Schütt 1895 (=*D. globulus* (Schütt) Balech 1967)
254 *Phalacroma hindmarchii* Murray *et* Whitting 1899 (=*D. hindmarchii* (Murray *et* Whitting) Balech 1967, non *Ph. hindmarchii* Pavillard 1916)
255 *Phalacroma jibbonense* Wood 1954 (=*D. jibbonensis* (Wood) Balech 1967)
256 *Phalacroma lativelatum* Kofoid *et* Skogsberg 1928 (=*D. lativelata* (Kofoid *et* Skogsberg) Balech 1967)
257 *Phalacroma dens* Kofoid *et* Skogsberg 1928 (=*D. lens* (Kofoid *et* Skogsberg) Balech 1967)
258 *Phalacroma mawsonii* Wood 1954 (=*D. mawsonii* (Wood 1954) Balech 1967,?*Ph. tuberculatum* Galil 1959)
259 *Phalacroma minutum* Cleve 1900 (=*D. minuta* (Cleve) Balech 1967)
260 *Phalacroma mitra* Schütt 1895 (=*D. mitra* (Schütt 1895) Abé *vel* Balech 1967, *Ph. rapa* Stein 1883, *Ph. dolichopterygium* Murray *et* Whitting 1899)
261 *Phalacroma monacanthum* Gail 1950 (non *D. monacantha* Kofoid *et* Skogsberg 1928)
262 *Phalacroma nasutum* Stein 1883 (=*Pseudophalacroma nasutum* (Stein) Jørgensen 1923, *D. nasutum* (Stein) Parke *et* Dixon 1968)
263 *Phalacroma operculatum* Stein 1883
264 *Phalacroma operculoides* Schütt 1895 (=*D. operculoides* (Schütt) Balech 1967)
265 *Phalacroma ovatum* (Claparède *et* Lachmann 1859) Jørgensen 1923
266 *Phalacroma parvulum* (Schütt 1895) Jørgensen 1923 (=*P. porodictyum* Stein var. *parvula* Schütt, *D. oviformis* Schiller 1928;?small cell of *D. rotundata*)
267 *Phalacroma porodictyum* Stein 1883
268 *Phalacroma praetextum* Kofoid *et* Michener 1911 (=*D. praetexta* (Kofoid *et* Michener) Balech 1967)
269 *Phalacroma protuberans* Kofoid *et* Skogsberg 1928 (=*D. protuberans* (Kofoid *et* Skogsberg) Balech 1967)
270 *Phalacroma pugiunculus* Jørgensen 1923 (=*D. pugiunculus* (Jørgensen) Balech 1967)
271 *Phalacroma pulchellum* Lebour 1922
**Phalacroma pulchrum* Kofoid *et* Michener 1911
**Phalacroma pyriforme* Kofoid *et* Skogsberg 1928
272 *Phalacroma rapa* Stein 1883 (=*D. rapa* (Stein) Balech 1967, *Ph. mitra* Okamura 1907)
273 *Phalacroma rotundatum* (Claparède *et* Lachmann 1859) Kofoid *et* Michener 1911 (=*D. rotundata* Claparède *et* Lachmann, *D. whittingae* Balech 1971, *Phalacroma rudgei* Murray *et* Whitting 1899, *D. rotundiformis* Tai *et* Skogsberg 1934)
274 *Phalacroma striatum* Kofoid 1907 (=*D. striata* (Kofoid) Balech 1967)
275 *Phalacroma tuberculatum* Galil 1959 (=*D. tuberculata* (Gail) Konovalova 1998,?*D. mawsonii* (Wood 1954) Balech 1988) [Konovalova (1998)]
276 *Phalacroma vastiforme* Tai *et* Skogsberg 1934 (=*D. vastiformis* (Tai *et* Skogsberg) Balech 1967)

Tab. 1. – continued

277 *Phalacroma vastum* Schütt 1895 (=*D. vasta* (Schütt) Balech 1967)
16 ***Sinophysis*** Nie *et* Wang 1944
278 *Sinophysis canaliculata* Quod, Ten-Hage, Turquet, Mascarell *et* Couté 1999 [Quod *et al.* (1999)]
279 *Sinophysis ebriola* (Herdman 1924) Balech 1956 (=*Phalacroma ebriola* Herdman 1924)
280 *Sinophysis grandis* Hoppenrath 2000 [Hoppenrath (2000c)]
281 *Sinophysis microcephala* Nie *et* Wang 1944
282 *Sinophysis stenosoma* Hoppenrath 2000 [Hoppenrath (2000c)]
17 ***Triposolenia*** Kofoid 1906 (10 species)
283 *Triposolenia ambulathrix* Kofoid 1907 (non *T. ambulathrix* Jørgensen 1923)
284 *Triposolenia bicornis* Kofoid 1906
285 *Triposolenia depressa* Kofoid 1906 (=*T. ambulathrix* Jørgensen 1923)
286 *Triposolenia exilis* Kofoid 1906
287 *Triposolenia fallax* Hernández-Becerril *et* Meave del Castillo 1999 [Hernández-Becerril and Meave del Castillo (1999)]
288 *Triposolenia fatula* Kofoid 1907
289 *Triposolenia intermedia* Kofoid *et* Skogsberg 1928
290 *Triposolenia longicornis* Kofoid 1907
291 *Triposolenia ramiciformis* Kofoid 1906
292 *Triposolenia truncata* Kofoid 1906

Oxyphysaceae Sournia 1984

18 ***Oxyphysis*** Kofoid 1926
293 *Oxyphysis oxytoxoides* Kofoid 1926

Gymnodiniales Lemmermann 1910

Gymnodiniaceae Lankester 1885

19 ***Akashiwo*** G. Hansen *et* Moestrup 2000 (=*Gymnodinium* Stein 1883 partim) [Daugbjerg *et al.* (2000)]
294 *Akashiwo sanguinea* (Hirasaka 1924) G. Hansen *et* Moestrup 2000 (=*G. sanguineum* Hirasaka, *G. splendens* Lebour 1925, *G. nelsonii* Martin 1929 [Daugbjerg *et al.* (2000), a feminine ending was used for the epithet, the use of "Akashio" is recommendable]
20 ***Amphidinium*** Claparède *et* Lachmann 1859 (76 species)
295 *Amphidinium acutum* Schiller 1928 (=*A. acutissimum* Schiller 1933)

Tab. 1. – continued

296 *Amphidinium aloxalocium* Norris 1961
297 *Amphidinium asymmetricum* Kofoid *et* Swezy 1921
**Amphidinium aureum* Böhm 1976
298 *Amphidinium bipes* Herdman 1924
299 *Amphidinium boggayum* S. Murray *et* Patterson 2002 [Murray and Patterson (2002)]
300 *Amphidinium britannicum* (Herdman 1924) Lebour 1925 (=*A. asymmetricum* var. *britannicum* Herdman 1922)
301 *Amphidinium carbunculus* Conrad *et* Kufferath 1954
302 *Amphidinium celestinum* Conrad *et* Kufferath 1954
303 *Amphidinium coeruleum* Conrad 1939
304 *Amphidinium conradii* (Conrad 1926) Schiller 1933 (=*Gymnodinium glaucum* Conrad)
**Amphidinium conus* Schiller 1928
305 *Amphidinium corallinum* Conrad *et* Kufferath 1954
306 *Amphidinium corpulentum* Kofoid *et* Swezy 1921
307 *Amphidinium corrugatum* J. Larsen *et* Patterson 1990
308 *Amphidinium crassum* Lohmann 1908 (=*A. phaeocysticola* Lebour 1925)
309 *Amphidinium cristatum* Ballantine *in* Parke *et* Dixon 1964 (=*A. rostratum* Conrad *et* Kufferath 1954)
310 *Amphidinium cucurbita* Kofoid *et* Swezy 1921
311 *Amphidinium cucurbitella* Kofoid *et* Swezy 1921
312 *Amphidinium curvatum* Schiller 1928
313 *Amphidinium cyaneoturbo* Conrad *et* Kufferath 1954
**Amphidinium dentatum* Kofoid *et* Swezy 1921
314 *Amphidinium discoidale* (Diesing 1866) Kofoid *et* Swezy 1921 (=*A. operculatum* var. *discoidalis* Diesing 1866)
315 *Amphidinium dubium* Conrad *et* Kufferath 1954
316 *Amphidinium emarginaum* (Diesing 1886) Kofoid *et* Swezy 1921 (=*A. operculatum* var. *marginata* Diesing 1886)
317 *Amphidinium extensum* Wulff 1916
**Amphidinium fastigium* Kofoid *et* Swezy 1921
**Amphidinium filum* Böhm 1976
318 *Amphidinium flagellans* Schiller 1928

Tab. 1. – continued

319 *Amphidinium flexum* Herdman 1923
**Amphidinium galbanum* Kofoid *et* Swezy 1921
320 *Amphidinium glabrum* Hopperanth *et* Okolodkov 2000 [Hoppenrath and Okolodkov (2000)]
321 *Amphidinium glaucum* Conrad 1926
322 *Amphidinium globosum* Schröder 1911
323 *Amphidinium hadai* Balech 1976 (=*A. acutissimum* Schiller sensu Hada 1970)
324 *Amphidinium herdmanii* Kofoid *et* Swezy 1921 (=*A. operculatum* Herdman 1911)
325 *Amphidinium incoloratum* P.H. Campbell 1973 (=*A. boekhoutnesis* Caljon 1983)
326 *Amphidinium inflatum* Kofoid 1931
327 *Amphidinium kesslitzii* Schiller 1928
328 *Amphidinium lacustre* Stein 1883 (=*A. lacustriforme* Schiller 1928, *A. schroederi* Schiller 1928)
329 *Amphidinium lanceolatum* Schröder 1911
330 *Amphidinium latum* Lebour 1925
331 *Amphidinium lilloense* Conrad *et* Kufferath 1954
332 *Amphidinium lissae* Schiller 1925
333 *Amphidinium longum* Lohmann 1908 (=*A. acutum* Lohmann 1920, non *Cochlodinium longum* Lohmann 1908, non *A. acutum* Schiller 1928)
334 *Amphidinium luteum* Skuja 1939
**Amphidinium machapungarum* P.H. Campbell 1973
335 *Amphidinium macrocephalum* Conrad *et* Kufferath 1954
336 *Amphidinium mammillatum* Conrad *et* Kufferath 1954 (=*A. pseudogalbanum* Conrad *et* Kufferath 1954)
337 *Amphidinium mananninii* Herdman 1924
338 *Amphidinium massartii* Biecheler 1952 (=*A. carterae* Hulburt 1957, non *A. klebsii* Kofoid *et* Swezy 1921)
339 *Amphidinium microcephalum* Norris 1961
340 *Amphidinium mootonorum* S. Murray *et* Patterson 2002 [Murray and Patterson (2002)]
341 *Amphidinium oceanicum* Lohmann 1920
342 *Amphidinium operculatum* Claparède *et* Lachmann 1859 (=*A. klebsii* Kofoid *et* Swezy 1921, *A. wislouchii* Hulburt 1957, *A. rhynchocephalum* Anissimowa 1926, *A. hoefleri* Schiller *et* Diskus 1955, *A. elegans* Grell *et* Wohlfarth-Bottermann 1957, *Amphidinium operculatum* var. *gibbosum* Maranda *et* Shimizu 1996)
343 *Amphidinium ornithocephalum* Conrad 1939

Tab. 1. – continued

344 *Amphidinium ovoideum* (Lemmermann 1896) Lemmermann 1900 (=*Prorocentrum ovoideum* Lemmermann)
345 *Amphidinium ovum* Herdman 1924
**Amphidinium pacificum* Kofoid *et* Swezy 1921
346 *Amphidinium pelagicum* Lebour 1925
347 *Amphidinium pellucidum* Herdman 1922 (=*A. subsalsum* Biecheler 1952)
348 *Amphidinium phthartum* Skuja 1939
349 *Amphidinium poecilochroum* J. Larsen 1985
350 *Amphidinium prismaticum* (Conrad 1926) Schiller 1933 (=*Trochodinium prismaticum* Conrad)
351 *Amphidinium psammophilum* Conrad *et* Kufferath 1954
352 *Amphidinium psittacus* J. Larsen 1985
353 *Amphidinium purpureum* Conrad *et* Kufferath 1954
354 *Amphidinium roseolum* (Schmarda 1854) Schiller 1933 (=*Gymnodinium roseolum* (Schmarda) Stein 1878)
355 *Amphidinium salinum* Ruinen 1938
356 *Amphidinium scissum* Kofoid *et* Swezy 1921 (=*A. scissoides* Lebour 1925)
357 *Amphidinium semilunatum* Herdman 1923 (=*Thecadinium semilunatum* (Herdman) Dodge 1982)
358 *Amphidinium semilunatum* Kofoid *et* Swezy 1921 (non *A. semilunatum* Herdman 1923, *Thecadinium inclinatum* Balech 1956)
359 *Amphidinium sphenoides* Wulff 1916 (=*Gymnodinium filum* Lebour 1917)
360 *Amphidinium steinii* Lemmemann 1910 (=*Amphidinium operculatum* Stein 1883)
361 *Amphidinium stellatum* Conrad *et* Kufferath 1954
362 *Amphidinium stigmatum* Schiller 1928
**Amphidinium sulcatum* Kofoid 1907
363 *Amphidinium testudo* Herdman 1924
364 *Amphidinium tortum* Conrad *et* Kufferath 1954
365 *Amphidinium trochodinoides* Conrad *et* Kufferath 1954
**Amphidinium truncatum* Kofoid *et* Swezy 1921
366 *Amphidinium turbo* Kofoid *et* Swezy 1921
367 *Amphidinium vasculum* Kofoid *et* Swezy 1921
368 *Amphidinium vitreum* Herdman 1924

Tab. 1. – continued

369 *Amphidinium vittatum* Conrad *et* Kufferath 1954
370 *Amphidinium yoorugurrum* S. Murray *et* Patterson 2002 [Murray and Patterson (2002)]
21 *Cochlodinium* Schütt 1896 (35 species)
371 *Cochlodinium achromaticum* Lebour 1925
372 *Cochlodinium adriaticum* Schiller 1933 (=*Gyrodinium adriaticum* Schiller 1928)
373 *Cochlodinium archimedes* (Pouchet 1883) Lemmermann 1899 (=*Gymnodinium archimedes* Pouchet)
**Cochlodinium atromaculatum* Kofoid *et* Swezy 1921 (non *Nematodinium atromaculatum* Kofoid 1931)
374 *Cochlodinium brandtii* Wulff 1916 (=*C. angustum* Kofoid *et* Swezy 1921)
375 *Cochlodinium catenatum* Okamura 1916 (=?*C. polykrikoides* Margalef 1961)
376 *Cochlodinium cavatum* Kofoid *et* Swezy 1921
377 *Cochlodinium cereum* Kofoid *et* Swezy 1921
378 *Cochlodinium citron* Kofoid *et* Swezy 1921
379 *Cochlodinium clarissimum* Kofoid *et* Swezy 1921
380 *Cochlodinium cnidophorum* Biecheler 1939
381 *Cochlodinium conspiratum* Kofoid *et* Swezy 1921
382 *Cochlodinium constrictum* (Schütt 1895) Lemmermann 1899 (=*Gymnodinium constrictum* Schütt)
383 *Cochlodinium convolutum* Kofoid *et* Swezy 1921
384 *Cochlodinium distortum* Kofoid *et* Swezy 1921
**Cochlodinium elongatum* Kofoid *et* Swezy 1921
385 *Cochlodinium faurei* Kofoid *et* Swezy 1921
386 *Cochlodinium flavum* Kofoid 1931 (non *Gymnodinium flavum* Kofoid *et* Swezy 1921, non *Gyrodinium flavum* Kofoid 1931)
387 *Cochlodinium geminatum* (Schütt 1895) Schütt 1896 (=*Gymnodinium geminatum* Schütt)
388 *Cochlodinium helicoides* Lebour 1925 (=*C. helix* Schütt 1895 partim, *Cochlodinium helix* Kofoid *et* Swezy 1921)
389 *Cochlodinium helix* (Pouchet 1887) Lemmermann 1899 (=*Gymnodinium helix* Pouchet, *Gymnodinium helix* Schütt 1895)
390 *Cochlodinium lebourae* Kofoid *et* Swezy 1921
**Cochlodinium moniliforme* Margalef 1968
391 *Cochlodinium pellucidum* Lohmann 1908
392 *Cochlodinium pirum* (Schütt 1895) Lemmermann 1899 (=*Gymnodinium pirum* Schütt)

Tab. 1. – continued

393 *Cochlodinium platycorne* Daday 1888
394 *Cochlodinium polykrikoides* Margalef 1961 (=*C. heterolobatum* E.S. Silva 1967, =?*C. catenatum* Okamura 1916)
395 *Cochlodinium pulchellum* Lebour 1917
396 *Cochlodinium pupa* Lebour 1925
397 *Cochlodinium radiatum* Kofoid *et* Swezy 1921
**Cochlodinium rosaceum* Kofoid *et* Swezy 1921
398 *Cochlodinium schuettii* Kofoid *et* Swezy 1921 (=*Gymnodinium helix* Schütt 1895 partim, non Pouchet 1887)
399 *Cochlodinium scintillans* Kofoid *et* Swezy 1921
400 *Cochlodinium semistriatum* Elbrächter 1979
401 *Cochlodinium strangulatum* (Schütt 1895) Schütt 1896 (=*Gymnodinium strangulatum* Schütt)
402 *Cochlodinium turbineum* Kofoid *et* Swezy 1921
403 *Cochlodinium vinctum* Kofoid *et* Swezy 1921
404 *Cochlodinium virescens* Kofoid *et* Swezy 1921
405 *Cochlodinium volutum* Kofoid *et* Swezy 1921
22 *Gymnodinium* Stein 1878 emend. G. Hansen *et* Moestrup 2000 (=*Gyrodinium* Kofoid *et* Swezy 1921 partim) (173 species) [Daugbjerg *et al.* (2000)]
406 *Gymnodinium achromaticum* Lebour 1917
407 *Gymnodinium adriaticum* (Schmarda 1846) Kofoid *et* Swezy 1921
408 *Gymnodinium aequatoriale* Hasle 1960
**Gymnodinium acutissimum* Okolodkov 1997 [Okolodkov (1997), not listed in Okolodkov (1998)]
409 *Gymnodinium agaricoides* P.H. Campbell 1973
410 *Gymnodinium agile* Kofoid *et* Swezy 1921 (non *G. agile sensu* Herdman 1922=*Herdmania litoralis* Dodge 1981)
411 *Gymnodinium agiliforme* Schiller 1928
412 *Gymnodinium alaskense* Bursa 1963
413 *Gymnodinium albidum* J.B. Lackey *et* E.W. Lackey 1970
414 *Gymnodinium allophron* J. Larsen 1994 [Larsen (1994)]
415 *Gymnodinium amphityphlum* J. Larsen 1994 [Larsen (1994)]
416 *Gymnodinium amphora* Kofoid *et* Swezy 1921
**Gymnodinium amplinucleum* P.H. Campbell 1973
417 *Gymnodinium arcticum* Wulff 1916 (=?*G. soyai* Hada 1970)

Tab. 1. – continued

418 *Gymnodinium arcuatum* Kofoid 1931
419 *Gymnodinium arenicolum* Dragesco 1965 (=*G. variabile* sensu Dodge 1982, non Herdman 1924)
420 *Gymnodinium atomatum* J. Larsen 1994 [Larsen (1994)]
421 *Gymnodinium attenuatum* Kofoid *et* Swezy 1921
422 *Gymnodinium aurantium* P.H. Campbell 1973
423 *Gymnodinium auratum* Kofoid *et* Swezy 1921
424 *Gymnodinium aureolum* (Hulburt 1957) G. Hansen 2000 (=*G. mikimotoi* sensu Hallegraeff 1991, non European *Gyrodinium aureolum* Hulburt sensu Braarud *et* Heimdal 1970, non *Karenia mikimotoi*) [Hansen *et al.* (2000)]
426 *Gymnodinium australense* Ruiner 1938
427 *Gymnodinium baccatum* Balech *in* Balech *et* El-Sayed 1965
**Gymnodinium bicaudatum* Pavillard 1905
428 *Gymnodinium biconicum* Schiller 1928 (non *Gyrodinium biconicum* Kofoid *et* Swezy 1921)
429 *Gymnodinium bicorne* Kofoid *et* Swezy 1921 (=*Dissodinium bicorne* (Kofoid *et* Swezy) F.J.R. Taylor 1976)
430 *Gymnodinium bifurcatum* Kofoid *et* Swezy 1921
431 *Gymnodinium bilobatum* van Meel 1969
432 *Gymnodinium birotundatum* van Goor 1925
433 *Gymnodinium boguense* P.H. Campbell 1973
434 *Gymnodinium bonaerense* Akselman 1985
**Gymnodinium boreale* Gaarder *in* Braarud *et al.* 1953
435 *Gymnodinium canus* Kofoid *et* Swezy 1921
436 *Gymnodinium capitatum* Conrad *et* Kufferath 1954
437 *Gymnodinium caput* Schiller 1928
438 *Gymnodinium cassiei* Norris 1961
439 *Gymnodinium catenatum* Graham 1943
440 *Gymnodinium chiasmonetrium* Norris 1961
441 *Gymnodinium chlorophorum* Elbrächter *et* Schnepf 1996 (=?*Lepidodinium viride* Watanabe *et al.* 1990) [Elbrächter and Schnepf (1996)]
442 *Gymnodinium chukwanii* Ballantine 1961
443 *Gymnodinium cinctum* Kofoid *et* Swezy 1921
444 *Gymnodinium cnodax* Conrad *et* Kufferath 1954

Tab. 1. – continued

445 *Gymnodinium coeruleum* Dogiel 1906 (=*Balechina coerulea* (Dogiel) F.J.R. Taylor 1976)
446 *Gymnodinium conicum* Kofoid *et* Swezy 1921 (=*G. viridis* Lebour 1917)
**Gymnodinium contractum* Kofoid *et* Swezy 1921
447 *Gymnodinium corii* Schiller 1928
448 *Gymnodinium costatum* Kofoid *et* Swezy 1921
449 *Gymnodinium cucumis* Schütt 1895
450 *Gymnodinium cyanea-fungiforme* Conrad *et* Kufferath 1954
451 *Gymnodinium danicans* P.H. Campbell 1973
452 *Gymnodinium dentatum* J. Larsen 1994 [Larsen (1994)]
453 *Gymnodinium diamantidium* Norris 1961
454 *Gymnodinium diplosonus* Schütt 1895
455 *Gymnodinium dissimile* Kofoid *et* Swezy 1921
456 *Gymnodinium enorme* Ballantine *in* Parke *et* Dixon 1964 (=*G. irregulare* Conrad *et* Kufferath 1954, non *G. irregulare* Hope 1954, nec Christen 1959)
**Gymnodinium dogielii* Kofoid *et* Swezy 1921
457 *Gymnodinium domaii* Kofoid *et* Swezy 1921
**Gymnodinium elongatum* Hope 1954 (non *Gyrodinium elongatum* Schiller 1955,?*Lessardia elongata* Saldarriaga *et* F.J.R. Taylor 2003) [Saldarriaga *et al.* (2003)]
458 *Gymnodinium endosciculum* P.H. Campbell 1973
459 *Gymnodinium enorme* Ballantine *in* Parke *et* Dixon 1964
460 *Gymnodinium excavatum* van Meel 1969 (non *G. excavatum* Nygaard 1954)
461 *Gymnodinium exechogloutum* Norris 1961
462 *Gymnodinium fissum* Levander 1894 (=*Spirodinium fissum* (Levander) Lemmermann 1900, non *Gyrodinium fissum* (Levander) Kofoid *et* Swezy 1921)
463 *Gymnodinium flavum* Kofoid *et* Swezy 1921 (non *Gyrodinium flavum* Kofoid 1931)
464 *Gymnodinium fossatum* Conrad *et* Kufferath 1954
465 *Gymnodinium frigidum* Balech *in* Balech *et* El-Sayed 1965
Gymnodinium fuscum (Ehrenberg 1834) Stein 1883 (=*G. caudatum* Prescot 1944, *Gymnocystodinium gessneri* Baumeister 1957, *Cystodinium gessneri* (Baumeister) Bourrelly 1970) [freshwater]

Tab. 1. – continued

466 *Gymnodinium fusus* Schütt 1896 (=*Gyrodinium falcatum* Kofoid *et* Swezy 1921 partim, *Gyrodinium sugashimanii* J. Cachon, H. Sato, M. Cachon *et* S. Sato 1989, *Pseliodinium vaubanii* Sournia 1972)

467 *Gymnodinium galatheanum* Braarud 1957 (non *Gyrodinium galatheanum* (Braarud) F.J.R. Taylor 1992, non *Karlodinium micrum* (Leadbeater *et* Dodge 1966) J. Larsen 2000) [Daugbjerg *et al.* 2000)]

468 *Gymnodinium galeaeforme* Matzenauer 1933
**Gymnodinium galeiforme* Okolodkov 1997 [Okolodkov (1997), not listed in Okolodkov (1998)]

469 *Gymnodinium galeatum* J. Larsen 1994 [Larsen (1994)]

470 *Gymnodinium galesianum* P.H. Campbell 1973

471 *Gymnodinium gelbum* Kofoid 1931

472 *Gymnodinium gibbera* Schiller 1928

473 *Gymnodinium glandiforme* Conrad *et* Kufferath 1954

474 *Gymnodinium gleba* Schütt 1895

475 *Gymnodinium gracile* Bergh 1881 (=*G. spirale* var. *nobilis* Pouchet 1883, *G. roseum* Lohmann 1908, *G. abbreviatum* Kofoid *et* Swezy 1921, *G. lohmannii* Paulsen 1908, non *G. roseum* Dogiel 1906)

476 *Gymnodinium gracilenium* P.H. Campbell 1973

477 *Gymnodinium granmaticum* (Pouchet 1887) Kofoid *et* Swezy 1921 (=*G. punctatum* var. *grammaticum* Pouchet)

478 *Gymnodinium guttiforme* J. Larsen 1994 [Larsen (1994)]

479 *Gymnodinium guttula* Balech 1976 (=*Gymnodinium cinctum* Kofoid *et* Swezy sensu Hada 1970)

480 *Gymnodinium halophilum* Biecheler 1952
**Gymnodinium herbaceum* Kofoid *in* Kofoid *et* Swezy 1921

481 *Gymnodinium heterostriatum* Kofoid *et* Swezy 1921 (=*G. lucidum* Ballantine *in* Parke *et* Dixon 1964, *G. hyalinum* Lebour 1925, non *G. striatissimum* Hulburt 1957)

482 *Gymnodinium hiroshimaense* Hada 1968

483 *Gymnodinium hulburtii* P.H. Campbell 1973

484 *Gymnodinium impudicum* (Fraga *et* Bravo 1995) G. Hansen *et* Moestrup 2000 [Fraga *et al.* (1995), Daugbjerg *et al.* (2000)]

485 *Gymnodinium incertum* Herdman 1924

486 *Gymnodinium incisum* Kofoid *et* Swezy 1921

487 *Gymnodinium incoloratum* Conrad *et* Kufferath 1954

488 *Gymnodinium inconstans* van Meel 1969

Tab. 1. – continued

489 *Gymnodinium intercalare* Bursa 1961
490 *Gymnodinium instriatum* (Freudenthal *et* Lee 1963) Coats 2002 (=*G. instriatum* Freudenthal *et* Lee) [Coats and Park (2002)]
491 *Gymnodinium irregulare* Hope 1954 (non *G. enorme* Ballantine *in* Parke *et* Dixon 1964,
non *Gymnodinium irregulare* Christen 1959=*G. uberrimum* (Allman 1855) Kofoid *et* Swezy 1921)
492 *Gymnodinium japonicum* Hada 1974
493 *Gymnodinium katodiniforme* Elbrächter 1979
494 *Gymnodinium kowalevskii* Pitzik 1967
495 *Gymnodinium lachmannii* Saville-Kent 1881
496 *Gymnodinium lanskoi* Rouchijajnen 1968
497 *Gymnodinium lazulum* Hulburt 1957
498 *Gymnodinium leptum* Norris 1961
499 *Gymnodinium lineatum* Kofoid *et* Swezy 1921
**Gymnodinium linedunicum* Kofoid *et* Swezy 1921
500 *Gymnodinium lira* Kofoid *et* Swezy 1921
501 *Gymnodinium loburiere* P.H. Campbell 1973
502 *Gymnodinium luteo-viride* van Meel 1969
503 *Gymnodinium magalonnense* Biecheler 1939
504 *Gymnodinium mammosum* van Meel 1969
505 *Balechina marianae* F.J.R. Taylor 1976 (to be transferred to *Gymnodinium*)
506 *Gymnodinium marinum* Saville-Kent 1881
507 *Gymnodinium maximum* Nordli 1951
508 *Gymnodinium metum* Hulburt 1957
509 *Gymnodinium microreticulatum* Bolch, Negri *et* Hallegraeff 1999 [Bolch *et al.* (1999)]
510 *Gymnodinium minus* Lebour 1917
511 *Gymnodinium minutulum* J. Larsen 1994 [Larsen (1994)]
512 *Gymnodinium modestum* Balech 1976 (=*Gymnodinium baccatum* Balech sensu Hada 1970)
513 *Gymnodinium multilineatum* Kofoid *et* Swezy 1921
514 *Gymnodinium multistriatum* Kofoid *et* Swezy 1921
515 *Gymnodinium najadum* Schiller 1928

Tab. 1. – continued

	**Gymnodinium uanum* Schiller 1928
516	*Gymnodinium natalense* Horiguchi *et* Pienaar 1994 [Horiguchi and Pienaar (1994a)]
517	*Gymnodinium neapolitanum* Schiller 1928
518	*Gymnodinium nolleri* Ellegaard *et* Moestrup 1999 [Ellegaard and Moestrup (1999)]
	**Gymnodinium nucaeum* Okolodkov 1997 [Okolodkov (1997), not listed in Okolodkov (1998)]
	**Gymnodinium obliquum* Okolodkov 1997 [Okolodkov (1997), not listed in Okolodkov (1998)]
519	*Gymnodinium oceanicum* Hasle 1960 (non *Gymnodinium oceanicum* Sukhanova 1968, non *Gyrodinium oceaniae* Okolodkov 1997)
520	*Gymnodinium ochraceum* Kofoid 1931
521	*Gymnodinium octo* J. Larsen 1994 [Larsen (1994)]
522	*Gymnodinium opressum* Conrad 1926
523	*Gymnodinium ordinatum* Skuja 1939
524	*Gymnodinium ostenfeldii* Schiller 1928
525	*Gymnodinium ovato-capitatum* van Meel 1969
	**Gymnodinium ovoideum* Okolodkov 1997 (non *Gyrodinium ovoideum* Kofoid *et* Swezy 1921) [Okolodkov (1997), not listed in Okolodkov (1998)]
526	*Gymnodinium ovulum* Kofoid *et* Swezy 1921
527	*Gymnodinium pachydermatum* Kofoid *et* Swezy 1921 (=*Balechina pachydermata* (Kofoid *et* Swezy) Loeblich Jr. *et* Loeblich III 1968)
528	*Gymnodinium pallidum* Skuja 1939
529	*Gymnodinium parvulum* J. Larsen 1994 [Larsen (1994)]
530	*Gymnodinium patagonicum* Balech 1971
531	*Gymnodinium paulsenii* Schiller 1928
532	*Gymnodinium perplexum* van Meel 1969
533	*Gymnodinium pigmentosum* (Dodge 1967) Loeblich III 1970 (=*Aureodinium pigmentosum* Dodge)
534	*Gymnodinium pingue* van Meel 1969 (non *Gyrodinium pingue* (Schütt 1895) Kofoid *et* Swezy 1921)
535	*Gymnodinium placidum* Herdman 1922
536	*Gymnodinium polycomma* J. Larsen 1994 [Larsen (1994)]
537	*Gymnodinium prolatum* J. Larsen 1994 [Larsen (1994)]
538	*Gymnodinium pulchrum* Schiller 1928
539	*Gymnodinium pumilum* J. Larsen 1994 [Larsen (1994)]

Tab. 1. – continued

540	*Gymnodinium punctatum* Pouchet 1887
541	*Gymnodinium puniceum* Kofoid *et* Swezy 1921
542	*Gymnodinium pygmaeum* Lebour 1925 (=?*Gyrodinium aureolum* Hulburt 1957)
543	*Gymnodinium pyrenoidosum* Horiguchi *et* Chihara 1988
544	*Gymnodinium pyrocystis* Jørgensen 1912 (=?*Kofoidinium splendens* J. Cachon *et* M. Cachon 1967)
545	*Gymnodinium quadrilobatum* Horiguchi *et* Pienaar 1994 [Horiguchi and Pienaar (1994b)]
546	*Gymnodinium radiatum* Kofoid *et* Swezy 1921
547	*Gymnodinium ravenescens* Kofoid *et* Swezy 1921
548	*Gymnodinium regulare* van Meel 1969
	**Gymnodinium rete* Schütt 1895
549	*Gymnodinium rhomboides* Schütt 1895
550	*Gymnodinium roseostigma* P.H. Campbell 1973
	**Gymnodinium rubricauda* Kofoid *et* Swezy 1921
551	*Gymnodinium rubrotinctum* Lebour 1925
552	*Gymnodinium rubrum* Kofoid *et* Swezy 1921
553	*Gymnodinium scaphium* van Meel 1969
554	*Gymnodinium schaefferi* Morris 1937
555	*Gymnodinium scopulosum* Kofoid *et* Swezy 1921
556	*Gymnodinium semidivisum* Schiller 1928
557	*Gymnodinium simplex* (Lohmann 1911) Kofoid *et* Swezy 1921 (=*Protodinium simplex* Lohmann 1908)
558	*Gymnodinium situla* Kofoid *et* Swezy 1921
	**Gymnodinium sphaericum* (Calkins 1902) Kofoid *et* Swezy 1921 (=*G. gracile* var. *sphaerica* Calkins)
559	*Gymnodinium sphaeroideum* Kofoid 1931
560	*Gymnodinium soyai* Hada 1970
561	*Gymnodinium stellatum* Hulbult 1957
562	*Gymnodinium subroseum* P.H. Campbell 1973
563	*Gymnodinium suffuscum* van Meel 1969 [?»subfuscum«]
564	*Gymnodinium sulcatum* Kofoid *et* Swezy 1921

Tab. 1. – continued

565 *Gymnodinium tehna* van Meel 1969
566 *Gymnodinium translucens* Kofoid *et* Swezy 1921 (non *Gymnodinium translucens* P.H. Campbell 1973)
567 *Gymnodinium translucens* P.H. Campbell 1973 (non *Gymnodinium translucens* Kofoid *et* Swezy 1921)
**Gymnodinium triangularis* Lebour 1917
568 *Gymnodinium uncatenatum* (Hulburt 1957) Hallegraeff 2002 [Hallegraeff (2002)]
569 *Gymnodinium valdecompressum* P.H. Campbell 1973
570 *Gymnodinium variabile* Herdman 1924 (non *G. variabile* sensu Dodge 1982)
571 *Gymnodinium vas* van Meel 1939
572 *Gymnodinium verruculosum* P.H. Campbell 1973
**Gymnodinium violescens* Kofoid *et* Swezy 1921 (non *Warnowia violescens* (Kofoid *et* Swezy) Lindemann 1928)
573 *Gymnodinium viride* Wood 1963 (non *Gymnodinium viridescens* Kofoid 1931)
**Gymnodinium viridescens* Kofoid 1931
574 *Gymnodinium vestifici* Schütt 1885 [=?*Katodinium glaucum* (Lebour 1917) Loeblich III 1965]
575 *Gymnodinium viridans* van Meel 1969
576 *Gymnodinium voukii* Schiller 1928
577 *Gymnodinium wilczekii* Pouchet 1894
578 *Gymnodinium wulffii* Schiller 1933 (non *Gyrodinium wulffii* Schiller 1933)
23 ***Gyrodinium*** Kofoid *et* Swezy 1921 emend. G. Hansen *et* Moestrup 2000 (=***Gymnodinium*** Stein 1878 partim) [Daugbjerg *et al.* (2000)] (87 species)
**Gyrodinium acicula(tum* G. Hansen *et* J. Larsen 1992
579 *Gyrodinium acutum* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium spirale* var. *acuta* Schütt)
580 *Gyrodinium antarcticum* Hasle 1960
581 *Gyrodinium apidiomorphum* Norris 1961
582 *Gyrodinium arcticum* Bursa 1961
583 *Gyrodinium ascendans* Kofoid 1931
584 *Gyrodinium atractos* J. Larsen 1996 [Larsen (1996)]
585 *Gyrodinium aureum* (Conrad 1926) Schiller 1933 (=*Spirodinium aureum* Conrad)
586 *Gyrodinium biconicum* Kofoid *et* Swezy 1921 (non *Gymnodinium biconicum* Schiller 1928)
587 *Gyrodinium bistellatum* Conrad *et* Kufferath 1954

Tab. 1. – continued

588 *Gyrodinium britannicum* Kofoid *et* Swezy 1921 (=*Spirodinium spirale* var. *acutum* Schütt sensu Lebour 1917)
**Gyrodinium californicum* Bursa 1962
589 *Gyrodinium calyptroglyphe* Lebour 1925 (=*Sclerodinium calyptoglyphe* (Lebour) Dodge 1981)
590 *Gyrodinium capsulatum* Kofoid *et* Swezy 1921
591 *Gyrodinium cartereiense* P.H. Campbell 1973
592 *Gyrodinium caudatum* Kofoid *et* Swezy 1921
593 *Gyrodinium citrinum* Kofoid 1931
594 *Gyrodinium chiasmonetrium* Norris 1961
595 *Gyrodinium cochlea* Lebour 1925
596 *Gyrodinium complanatum* P.H. Campbell 1973
**Gyrodinium concentricum* (Lebour 1917) Kofoid *et* Swezy 1921 (=*Spirodinium concentricum* Lebour)
597 *Gyrodinium conicum* Schiller 1928
598 *Gyrodinium contortum* (Schütt 1895) Kofoid *et* Swezy 1921 (=*G. contortum* Schütt, *Gymnodinium opimum* Schütt 1895 partim)
599 *Gyrodinium corallinum* Kofoid *et* Swezy 1921
600 *Gyrodinium cornutum* (Pouchet 1885) Kofoid *et* Swezy 1921 (=*Gymnodinium spirale* var. *cornutum* Pouchet, non *G. cornutum* Schütt 1895)
601 *Gyrodinium corsicum* Paulmier, Berland, Billard *et* Nezan 1995 [resembles *Karlodinium micrum*] [Paulmier *et al.* (1995)]
602 *Gyrodinium crassum* (Pouchet 1885) Kofoid *et* Swezy 1921 (=*Gymnodinium crassum* Pouchet)
**Gyrodinium culeus* Kofoid *et* Swezy 1921
603 *Gyrodinium cuneatum* Kofoid *et* Swezy 1921 [=*Gymnodinium gracile* Bergh 1881]
604 *Gyrodinium dominans* Hulburt 1957
605 *Gyrodinium dorsum* Kofoid *et* Swezy 1921
606 *Gyrodinium estuariale* Hulburt 1957
607 *Gyrodinium falcatum* Kofoid *et* Swezy 1921 (=*Gymnodinium fusus* Schütt 1896 partim,
Gyrodinium sugashimanii J. Cachon, H. Sato, M. Cachon *et* S. Sato 1989, *Pseliodinium vaubanii* Sournia 1972)
608 *Gyrodinium ferrugineum* Kofoid 1931
609 *Gyrodinium fissoides* Elbrächter 1979 [=*G. fissum* (Levander 1894) Kofoid *et* Swezy 1921, non *Gymnodinium fissum* Levander 1894]
610 *Gyrodinium flagellare* Schiller 1928
**Gyrodinium flavescens* Kofoid *et* Swezy 1921

Tab. 1. – continued

	**Gyrodinium flavidum* Kofoid *et* Swezy 1921
611	*Gyrodinium flavum* Kofoid 1931 (non *Gymnodinium flavum* Kofoid *et* Swezy 1921)
612	*Gyrodinium foliaceum* Kofoid *et* Swezy 1921 (=*Gymnodinium viride* Schütt 1895, non *G. viride* Pénard 1891)
613	*Gyrodinium formosum* P.H. Campbell 1973
614	*Gyrodinium fulvum* Kofoid *et* Swezy 1921
615	*Gyrodinium fusus* (Meunier 1910) Akselman 1985 (=*Spirodinium fusus* Meunier, *Gyrodinium fusiforme* Kofoid *et* Swezy 1921)
616	*Gyrodinium glaciale* Hada 1970 *ex* Balech 1976
617	*Gyrodinium glaebum* Hulburt 1957
618	*Gyrodinium grave* (Meunier 1910) Kofoid *et* Swezy 1921 (=*Spirodinium grave* Meunier)
619	*Gyrodinium grenlandicum* Braarud 1935
620	*Gyrodinium grossestriatum* P.H. Campbell 1973
621	*Gyrodinium gutrula* J. Larsen 1996 (non *Gymnodinium guttula* Balech 1976) [Larsen (1996)]
622	*Gyrodinium herbaceum* Kofoid *et* Swezy 1921
623	*Gyrodinium heterogrammum* J. Larsen 1996 [Larsen (1996)]
624	*Gyrodinium impendens* J. Larsen 1996 (=*Gyrodinium impendens* G. Hansen *et* J. Larsen 1992) [Larsen (1996)]
	**Gyrodinium intortum* Kofoid *et* Swezy 1921
625	*Gyrodinium katodiniascens* P.H. Campbell 1973
626	*Gyrodinium kofoidii* Norris 1961
627	*Gyrodinium lachryma* (Meunier 1910) Kofoid *et* Swezy 1921 (=*Spirodinium lachryma* Meunier)
628	*Gyrodinium lebourae* Herdman 1924
629	*Gyrodinium leptogrammum* J. Larsen 1996 [Larsen (1996)]
630	*Gyrodinium lingulifera* Lebour 1925
631	*Gyrodinium longum* (Lohmann 1908) Kofoid *et* Swezy 1921 (=*Cochlodinium longum* Lohmann, non *Amphidinium longum* Lohmann 1908)
632	*Gyrodinium louisae* Conrad *et* Kufferath 1954
633	*Gyrodinium maculatum* Kofoid *et* Swezy 1921 (non *Warnowia maculata* (Kofoid *et* Swezy 1921) Lindemann 1928)
	**Gyrodinium melo* Kofoid *et* Swezy 1921
634	*Gyrodinium metum* Hulburt 1957
635	*Gyrodinium mitrum* Kofoid *et* Swezy 1921 (=*G. spirale* var. *mitra* Schütt 1895)

Tab. 1. – continued

636 *Gyrodinium mundulum* P.H. Campbell 1973
637 *Gyrodinium nasutum* (Wulff 1916) Schiller 1933
638 *Gyrodinium oblongum* J. Larsen *et* Patterson 1990
639 *Gyrodinium obtusum* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium spirale* Bergh var. *obtusa* Schütt, non *G. spirale* var. *obtusum* Dogiel 1906)
**Gyrodinium oceaniae* Okolodkov 1997 (non *Gymnodinium oceanicum* Hasle 1960) [Okolodkov (1997), not listed in Okolodkov (1998)]
640 *Gyrodinium ochraceum* Kofoid *et* Swezy 1921
641 *Gyrodinium opimum* (Schütt 1895) Lebour 1925 (=*Gymnodinium opimum* Schütt, *Gyrodinium contortum* (Schütt) Kofoid *et* Swezy 1921 partim)
642 *Gyrodinium ovatum* (Gourret 1883) Kofoid *et* Swezy 1921 (=*Gymnodinium ovatum* Gourret)
**Gyrodinium ovoideum* Kofoid *et* Swezy 1921 (non *Gymnodinium ovoideum* Okolodkov 1997)
643 *Gyrodinium ovum* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium ovum* Schütt)
644 *Gyrodinium parvulum* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium parvulum* Schütt)
645 *Gyrodinium pavillardii* Biecheler 1934 (= *?Gymnodinium fissum* Levander 1894)
646 *Gyrodinium pellucidum* (Wulff 1916) Schiller 1933
647 *Gyrodinium pepo* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium spirale* var. *pepo* Schütt)
648 *Gyrodinium phorkorium* Norris 1961
649 *Gyrodinium pingue* (Schütt 1895) Kofoid *et* Swezy 1921 (=*Gymnodinium spirale* var. *pinguis* Schütt, *Spirodinium varians* Wulff 1916)
**Gyrodinium postmaculatum* Kofoid *et* Swezy 1921
650 *Gyrodinium prunus* (Wulff 1920) Lebour 1925 (=*Spirodinium prunus* Wulff)
651 *Gyrodinium resplendens* Hulburt 1957
652 *Gyrodinium rubricaudatum* Kofoid *et* Swezy 1921
653 *Gyrodinium schuettii* (Lemmermann 1899) Kofoid *et* Swezy 1921 (=*Spirodinium schuettii* Lemmermann, *Gymnodinium cornutum* Schütt 1895)
654 *Gyrodinium spirale* (Bergh 1881) Kofoid *et* Swezy 1921
**Gyrodinium spumantia* Kofoid *et* Swezy 1921
655 *Gyrodinium striatissimum* (Hulburt 1957) G. Hansen *et* Moestrup 2000 (=*G. striatissimum* Hulburt, non *Gymnodinium heterostriatum* Kofoid *et* Swezy 1921) [Daugbjerg *et al.* (2000)]
**Gyrodinium? striatum* (Dodge 1981)? (=*Sclerodinium striatum* Dodge 1981, *Gyrodinium calyptroglyphe* sensu Elbrächter 1979)
656 *Gyrodinium submarinum* Kofoid *et* Swezy 1921
**Gyrodinium truncatum* Kofoid *et* Swezy 1921

Tab. 1. – continued

657 *Gyrodinium truncus* Kofoid *et* Swezy 1921
658 *Gyrodinium undulans* Hulburt 1957
659 *Gyrodinium varians* (Wulff 1916) Schiller 1933 (non *Gymnodinium varians* Maskel 1887)
660 *Gyrodinium vesiculosum* J. Larsen 1996 [Larsen (1996)]
661 *Gyrodinium virgatum* Kofoid *et* Swezy 1921
662 *Gyrodinium viridescens* Kofoid *et* Swezy 1921
663 *Gyrodinium vorax* Biecheler 1952
664 *Gyrodinium wulffii* Schiller 1933 (non *Gymnodinium wulffii* Schiller 1933)
665 *Gyrodinium zeta* J. Larsen 1996 [Larsen (1996)]
24 ***Karenia*** G. Hansen *et* Moestrup 2000 (=*Gymnodinium* Stein 1878 partim) [Daugbjerg *et al.* (2000)] (8 species)
666 *Karenia bicuneiformis* Botes, Sym *et* Pitcher 2003 [Botes *et al.* (2003)]
667 *Karenia brevis* (Davis 1948) G. Hansen *et* Moestrup 2000 (=*Gymnodinium breve* Davis, *Ptychodiscus brevis* (Davis) Steidinger 1979) [Daugbjerg *et al.* (2000)]
668 *Karenia brevisulcata* (F.H. Chang 1999) G. Hansen *et* Moestrup 2000 (=*Gymnodinium brevisulcatum* F.H. Chang) [Chang (1999), Daugbjerg *et al.* (2000)]
669 *Karenia cristata* Botes, Sym *et* Pitcher 2003 [Botes *et al.* (2003)]
670 *Karenia digitata* Yang, Takayama, Matsuoka *et* Hodgkiss 2000 [Yang *et al.* (2000)]
671 *Karenia longicanalis* Yang, Hodgkiss *et* G. Hansen 2001 [Yang *et al.* (2001)]
672 *Karenia mikimotoi* (Miyake *et* Kominami *ex* Oda 1935) G. Hansen *et* Moestrup 2000 (=*G. nagasakiense* Takayama *et* Adachi 1984, *Gyrodinium aureolum* sensu Tangen *et* Bjornland 1981, non *Gyrodinium aureolum* Hulbult 1957, non *G. aureolum* (Hulbult) G. Hansen 2000) [Hansen *et al.* (2000)]
673 *Karenia umbella* de Salas, Bolch *et* Hallegraeff 2003 [Botes *et al.* (2003)]
25 ***Karlodinium*** J. Larsen 2000 (=***Gymnodinium*** Stein 1878 partim, ***Gyrodinium*** Kofoid *et* Swezy 1921 partim) [Daugbjerg *et al.* (2000)]
674 *Karlodinium micrum* (Leadbeater *et* Dodge 1966) J. Larsen 2000 (=*Woloszynskia micra* Leadbeater *et* Dodge, *G. micrum* (Leadbeater *et* Dodge) Loeblich III 1970, *G. galatheanum* Braarud sensu Kite *et* Dodge 1988, *Gyrodinium galatheanum* (Braarud 1957) F.J.R. Taylor 1992, non *Gymnodinium galatheanum* Braarud) [Daugbjerg *et al.* (2000)]
675 *Karlodinium veneficum* (Ballantine 1956) J. Larsen 2000 (=*Gymnodinium veneficum* Ballantine 1956) [Daugbjerg *et al.* (2000)]
676 *Karlodinium vitiligo* (Ballantine 1956) J. Larsen 2000 (=*Gymnodinium vitiligo* Ballantine,?*K. veneficum* (Ballantine) J. Larsen) [Daugbjerg *et al.* (2000)]

Tab. 1. – continued

26 ***Katodinium*** Fott 1857 (=***Massartia*** Conrad 1926) [some brackish/freshwater species included] (11 species)
677 *Katodinium asymmetricum* (Massart 1900) Loeblich III 1965 (=*Gymnodinium asymmetricum* Massart)
678 *Katodinium dorsalisulcum* Hulburt, McLaughlin *et* Zahl 1960
679 *Katodinium galeatum* (Conrad *et* Kufferath 1954) Loeblich III 1965 (=*Massartia galeata* Conrad *et* Kufferath)
680 *Katodinium glandula* (Herdman 1924) Loeblich III 1965 (=*Gymnodinium glandula* Herdman)
681 *Katodinium glaucum* (Lebour 1917) Loeblich III 1965 (=*Gyrodinium glaucum* (Lebour) Kofoid *et* Swezy 1921, *Spirodinium glaucum* Lebour, *Massartia glauca* Schiller 1933)
682 *Katodinium nieuportense* (Conrad 1926) Loeblich Jr. *et* Loeblich III 1966 (=*Massartia nieuportensis* Conrad)
683 *Katodinium pluristigmatum* P.H. Campbell 1973
684 *Katodinium ruppiae* (Conrad 1939) Loeblich III 1965 (=*Massartia ruppiae* Conrad)
685 *Katodinium thiophilum* (Conrad 1939) Loeblich III 1965 (=*Massartia thiophila* Conrad)
686 *Katodinium tubulatum* (Rampi 1969) Sournia 1973 (=*Massartia tubulata* Rampi)
687 *Katodinium uncinatum* (Kufferath 1957) Loeblich III 1965 (=*Massartia uncinata* Kufferath)
27 ***Lepidodinium*** Watanabe, Suda, Inouye, Sawaguchi *et* Chihara 1990
688 *Lepidodinium viride* Watanabe, Suda, Inouye, Sawaguchi *et* Chihara 1990 (=?*Gymnodinium chlorophorum* Elbrächter *et* Schnepf 1996)
Pavillardia* Kofoid *et* Swezy *in* Kofoid 1921
**Pavillardia tentaculifera* Kofoid *et* Swezy 1921
28 ***Pheopolykrikos*** Chatton 1933 emend. Matsuoka *et* Fukuyo 1986
689 *Pheopolykrikos beauchampii* Chatton 1933 (=*Polykrikos beauchampii* (Chatton) Dodge 1982)
690 *Pheopolykrikos hartmannii* (Zimmermann 1930) Matsuoka *et* Fukuyo 1986 (=*Polykrikos barnegatensis* Martin 1929)
29 ***Plectodinium*** Biecheler 1934
691 *Plectodinium nucleovolvatum* Biecheler 1934 (=*Gyrodinium rhabdomante* Balech 1973,?*Plectodinium miniatum* (Kofoid *et* Swezy 1921) F.J.R. Taylor 1980, *Cochlodinium miniatum* Kofoid *et* Swezy)
30 ***Takayama*** de Salas, Bolch, Botes *et* Hallegraeff 2003 (=***Gymnodinium*** Stein 1878 partim, ***Gyrodinium*** Kofoid *et* Swezy 1921 partim) [de Salas *et al.* (2003)] (lacking the ending, i.e. Takayamaea)
692 *Takayama acrotrochum* (Larsen 1996) de Salas, Bolch *et* Hallegraeff 2003 (=*Gyrodinium acrotrochum* Larsen) [J. Larsen (1996), de Salas *et al.* (2003)]
693 *Takayama cladochroma* (J. Larsen 1996) de Salas, Bolch *et* Hallegraeff 2003 (=*Gyrodinium cladochroma* Larsen) [J. Larsen (1996), de Salas *et al.* (2003)]

Tab. 1. – continued

694 *Takayama helix* de Salas, Bolch, Botes *et* Hallegraeff 2003 [de Salas *et al.* (2003)]
695 *Takayama pulchella* (J. Larsen 1994) de Salas, Bolch *et* Hallegraeff 2003 (=*Gymnodinium pulchellum* Larsen) [J. Larsen (1994), de Salas *et al.* (2003)]
696 *Takayama tasmanica* de Salas, Bolch *et* Hallegraeff 2003 [de Salas et *al.* (2003)] (published as »tasmanica«, ICBN Art. 23.5 and 32.5)
31 ***Torodinium*** Kofoid *et* Swezy 1921
697 *Torodinium robustum* Kofoid *et* Swezy 1921 (=*Gymnodinium teredo* Schütt 1895 partim)
698 *Torodinium teredo* (Pouchet 1885) Kofoid *et* Swezy 1921 (=*Gymnodinium teredo* Pouchet, *Torodinium robustum* Kofoid *et* Swezy 1921 partim)

Polykrikaceae Kofoid *et* Swezy 1921

32 ***Polykrikos*** Bütschli 1873
**Polykrikos grassei* Lecal 1972
699 *Polykrikos kofoidii* Chatton 1914 (=*P. schwarzii* Kofoid 1907)
700 *Polykrikos lebourae* Herdman 1924 (=*P. schwarzii* Herdman 1922)
701 *Polykrikos schwartzii* Bütschli 1873 (=*P. auricularia* Bergh 1881)

Ptychodiscaceae Lemmermann 1899

33 ***Ptychodiscus*** Stein 1883
702 *Ptychodiscus noctiluca* Stein 1883 (=*P. inflatus* Pavillard 1916, *P. carinatus* Kofoid 1907)

Warnowiaceae Lindemann 1928

34 ***Erythropsidinium*** P.C. Silva 1960 (=***Erythropsis*** Hertwig 1884, ***Pouchetia*** Schütt 1895 partim)
703 *Erythropsidinium agile* (Hertwig 1884) P.C. Silva 1960 (=*E. agilis* Hertwig, *E. pavillardii* (Kofoid *et* Swezy 1921) P.C. Silva 1960, *Erythropsis agilis* Pavillard 1905, *E.* (*Erythropsis*) *hispidum* (Kofoid *et* Swezy 1921) P.C. Silva 1960, *E.* (*Pouchetia*) *cornutum* (Schütt 1895) P.C. Silva 1960, *E.* (*Erythropsis*) *labrum* (Kofoid *et* Swezy 1921) P.C. Silva 1960, *E.* (*Erythropsis*) *scarlatinum* (Kofoid *et* Swezy 1921) P.C. Silva 1960, *E. richardii* (Kofoid *et* Swezy 1921) P.C. Silva 1960)
704 *Erythropsidinium cochlea* (Schütt 1895) P.C. Silva 1960 (=*Pouchetia cochlea* Schütt)
705 *Erythropsidinium extrudens* (Kofoid *et* Swezy 1921) P.C. Silva 1960 (=*E. extrudens* Kofoid *et* Swezy)
706 *Erythropsidinium minus* (Kofoid *et* Swezy 1921) P.C. Silva 1960 (=*E. minor* Kofoid *et* Swezy)
******Greuetodinium*** Loeblich III 1980 (=***Leucopsis*** Greuet 1968)
**Greuetodinium cylindricum* (Greuet 1968) Loeblich III 1980 (=*Leucopsis cylindrica* Greuet)
35 ***Nematodinium*** Kofoid *et* Swezy 1921 (=***Pouchetia*** Schütt 1895)

Tab. 1. – continued

707 *Nematodinium armatum* (Dogiel 1906) Kofoid *et* Swezy 1921 (=*P. armata* Dogiel, *P. maculata* Kofoid *et* Swezy 1921, *Nematodinium lebourae* Schiller 1933)
708 *Nematodinium atromaculatum* Kofoid 1931 (non *Cochlodinium atromaculatum* Kofoid *et* Swezy 1921)
709 *Nematodinium partitum* Kofoid *et* Swezy 1921
710 *Nematodinium torpedo* Kofoid *et* Swezy 1921
Nematopsides* Greuet 1973
**Nematopsides tentaculoides* Greuet 1973
36 *Proterythropsis* Kofoid *et* Swezy 1921
711 *Proterythropsis crassicaudata* Kofoid *et* Swezy 1921
712 *Proterythropsis vigilans* Marshall 1925 (=*Nematopsides vigilans* (Marshall) Greuet 1973)
Protopsis* Kofoid *et* Swezy 1921
**Protopsis elongata* Schiller 1928
**Protospis neapolitana* Kofoid *in* Kofoid *et* Swezy 1921
**Protospis nigra* (Pouchet 1887) Kofoid *et* Swezy 1921 (=*Gymnodinium polyphemus* var. *nigrum* Pouchet, *Pouchetia nigra* Lemmermann 1899)
**Protospis ochrea* (Wright 1907) Kofoid *et* Swezy 1921 (=*Pouchetia ochrea* Wright)
**Protospis simplex* Lebour 1925
37 *Warnowia* Lindemann 1928 (=***Pouchetia*** Schütt 1895, ***Protopsis*** Kofoid *et* Swezy 1921) (25 species)
713 *Warnowia alba* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. alba* Kofoid *et* Swezy)
714 *Warnowia atra* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. atra* Kofoid *et* Swezy)
715 *Warnowia compacta* (Schütt 1895) Schiller 1933 (=*P. compacta* Schütt, *P. contorta* Schütt 1895)
716 *Warnowia dohrnii* Zimmermann 1930
717 *Warnowia fusus* (Schütt 1895) Lindemann 1928 (=*P. fusus* Schütt)
718 *Warnowia hataii* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. hataii* Kofoid 1931)
719 *Warnowia juno* (Schütt 1895) Schiller 1933 (=*P. juno* Schütt, *P. nigra* Pavillard 1905 partim)
720 *Warnowia maculata* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. maculata* Kofoid *et* Swezy 1921, non *Gyrodinium maculatum* Kofoid *et* Swezy 1921)
721 *Warnowia maxima* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. maxima* Kofoid *et* Swezy)
722 *Warnowia mutsui* (Kofoid 1931) Schiller 1933 (=*P. mutsui* Kofoid)
723 *Warnowia panamensis* (Kofoid 1907) Schiller 1933 (=*P. panamensis* Kofoid)

Tab. 1. – continued

724 *Warnowia parva* (Lohmann 1908) Lindemann 1928 (=*P. parva* Lohmann)
725 *Warnowia polyphemus* (Pouchet 1895) Schiller 1933 (=*P. polyphemus* (Pouchet) Kofoid *et* Swezy 1921, *Gymnodinium polyphemus* Pouchet, *Warnowia pulchra* Schiller sensu Greuet 1968)
726 *Warnowia pouchetii* Schiller 1933 (=*P. pouchetii* Kofoid *et* Swezy 1921)
727 *Warnowia pulchra* (Schiller 1928) Schiller 1933 (=*P. pulchra* Schiller, non *W. pulchra* Schiller sensu Greuet 1968)
728 *Warnowia purpurata* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. perforata* Kofoid *et* Swezy)
729 *Warnowia purpurescens* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. purpurescens* Kofoid *et* Swezy)
730 *Warnowia reticulata* (Kofoid 1931) Schiller 1933 (=*P. reticulata* Kofoid)
731 *Warnowia rosea* (Pouchet 1879) Kofoid *et* Swezy 1921 (=*Gymnodinium polyphemus* var. *roseum* Pouchet, non *P. rosea* Schütt 1895)
732 *Warnowia rubescens* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. rubescens* Kofoid *et* Swezy)
733 *Warnowia schuettii* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. rosea* Schütt 1895)
734 *Warnowia striata* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. striata* Kofoid *et* Swezy)
735 *Warnowia subnigra* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. subnigra* Kofoid *et* Swezy)
736 *Warnowia violescens* (Kofoid *et* Swezy 1921) Lindemann 1928 (=*P. violescens* Kofoid *et* Swezy, non *Gymnodinium violescens* Kofoid *et* Swezy 1921)
737 *Warnowia voracis* (Kofoid *et* Swezy 1921) Schiller 1933 (=*P. voracis* Kofoid *et* Swezy)

Gymnodiniales *incertae sedis*

38 ***Ceratoperidinium*** Margalef 1969
738 *Ceratoperidinium yeye* Margalef 1969 (=*C. margalefii* Loeblich III 1980, *C. mediterraneum* Abboud-Abi Saab 1989) [see Gómez *et al.* (2004)]

Noctilucales Haeckel 1894

Kofoidiniaceae F.J.R. Taylor 1976

39 ***Cymbodinium*** J. Cachon *et* M. Cachon 1967
739 *Cymbodinium elegans* J. Cachon *et* M. Cachon 1967
40 ***Kofoidinium*** Pavillard 1928 (5 species)
740 *Kofoidinium arcticum* Bursa 1964
741 *Kofoidinium lebourae* (Pavillard 1921) F.J.R. Taylor 1976 (=*Gymnodinium lebourae* Pavillard, *G. pseudonoctiluca* Lebour 1917,?*G. fulgens* Kofoid *et* Swezy 1921)
742 *Kofoidinium pavillardii* J. Cachon *et* M. Cachon 1967 (=*Gymnodinium pseudonoctiluca* Pouchet 1885 partim, non *G. pseudonoctiluca* Lebour 1917)

Tab. 1. – continued

743 *Kofoidinium splendens* J. Cachon *et* M. Cachon 1967
744 *Kofoidinium velelloides* Pavillard 1928
41 ***Pomatodinium*** J. Cachon *et* Cachon-Enjumet 1966
745 *Pomatodinium impatiens* J. Cachon *et* Cachon-Enjumet 1966
42 ***Spatulodinium*** J. Cachon *et* M. Cachon 1968 (=***Gymnodinium*** Stein 1878 partim)
746 *Spatulodinium pseudonoctiluca* (Pouchet 1885) J. Cachon *et* M. Cachon *ex* Loeblich Jr. *et* Loeblich III 1969 (=*G. pseudonoctiluca* Pouchet, *G. fulgens* Kofoid *et* Swezy 1921,?*Amphidiniopsis urnaeformis* Gail 1950)

Leptodiscaceae Kofoid 1905

43 ***Cachonodinium*** Loeblich III 1980 (=***Leptodinium*** J. Cachon *et* M. Cachon 1969)
747 *Cachonodinium caudatum* (J. Cachon *et* M. Cachon 1969) Loeblich III 1980 (=*Leptodinium caudatum* J. Cachon *et* M. Cachon)
44 ***Craspedotella*** Kofoid 1905
748 *Craspedotella pileolus* Kofoid 1905
45 ***Leptodiscus*** Hertwig 1877 (=?***Pratjetella*** Lohmann 1920)
749 *Leptodiscus medusoides* Hertwig 1877 (=?*Pratjetella medusoides* (Hertwig) Loeblich Jr. *et* Loeblich III 1966)
46 ***Leptophyllus*** J. Cachon *et* Cachon-Enjumet 1964 (=***Abedinium*** Loeblich Jr. *et* Loeblich III 1966)
750 *Leptophyllus dasypus* J. Cachon *et* Cachon-Enjumet 1964 (=*Abedinium dasypus* (J. Cachon *et* Cachon-Enjumet) Loeblich Jr. *et* Loeblich III 1966)
47 ***Petalodinium*** J. Cachon *et* M. Cachon 1969
751 *Petalodinium porcelio* J. Cachon *et* M. Cachon 1969
48 ***Scaphodinium*** Margalef 1963 (=***Leptospathium*** J. Cachon *et* Cachon-Enjumet 1964)
752 *Scaphodinium mirabile* Margalef 1963 (=*Leptospathium navicula* J. Cachon *et* Cachon-Enjumet 1964)

Noctilucaceae Saville-Kent 1881

49 ***Noctiluca*** Suriray *ex* Lamarck 1816
753 *Noctiluca scintillans* (Macartney 1810) Kofoid 1920 (=*Noctiluca miliaris* Suriray *ex* Lamarck 1816)

Protodiniferaceae Kofoid *et* Swezy 1921

50 ***Pronoctiluca*** Fabre-Domergue 1889 [no dinokaryotic nucleus, the consideration as a dinoflagellate requires further research]
**Pronoctiluca acuta* (Lohmann 1912) Schiller 1933 (=*Rhynchomonas acuta* Lohmann 1912, *R. curvata* Lohmann 1921)
754 *Pronoctiluca pelagica* Fabre-Domergue 1889 (=*Rhynchomonas marina* Lohmann 1902, *Pelagorhynchus marinus* Pavillard 1917, =?*P. spinifera*)

Tab. 1. – continued

**Pronoctiluca phaeocysticola* (Scherffel 1900) Pavillard 1922 (=*Oxyrrhis phaeocysticola* Scherffel)
**Pronoctiluca rostrata* F.J.R. Taylor 1976 [related to *Lessardia* Saldarriaga *et* F.J.R. Taylor 2003]
755 *Pronoctiluca spinifera* (Lohmann 1920) Schiller 1933 (=*Protodinifer tentaculata* Kofoid *et* Swezy 1921,?*P. pelagica* Fabre-Domergue 1889)

Oxyrrhinales Sournia 1984 [the consideration as a dinoflagellate requires further research]

Oxyrrhinaceae Sournia 1984

51 ***Oxyrrhis*** Dujardin 1841
756 *Oxyrrhis marina* Dujardin 1841 (=*O. maritima* van Meel 1969, *O. tentaculifera* Conrad 1939)

Peridiniales Haeckel 1894

Amphidomataceae Sournia 1984

52 ***Amphidoma*** Stein 1883 (=***Pavillardinium*** De-Toni 1936 partim, ***Murrayella*** Kofoid 1907)
757 *Amphidoma acuminata* Stein 1883
758 *Amphidoma caudata* Halldal 1953 (=*Oxytoxum tonollii* Rampi 1969, *O. margalefii* Rampi 1969)
**Amphidoma curtata* Kofoid *et* Swezy 1911
**Amphidoma depressa* Kofoid *et* Swezy 1911
759 *Amphidoma elongata* Kofoid *et* Swezy 1911
**Amphidoma laticincta* Kofoid *et* Swezy 1911
760 *Amphidoma nucula* Stein 1883 (=*A. spinosa* (Kofoid 1907) Kofoid *et* Michener 1911, *Gonyaulax rouchii* Rampi 1948, *Pavillardinium spinosum* (Kofoid 1907) F.J.R. Taylor 1967 *ex* Sournia 1973, *Murrayella spinosa* Kofoid 1907)
**Amphidoma obtusa* Kofoid *et* Swezy 1911
761 *Amphidoma steinii* Schiller 1929

Ceratiaceae Kofoid 1907

53 ***Ceratium*** Schrank 1793 [the delimitation of species or infraespecific taxa strongly varies among authors] (63 species)
**Ceratium angustum* A.S. Campbell 1934
762 *Ceratium arcticum* (Ehrenberg 1854) Cleve 1901 (=*C. labradoricum* Vanhöffen 1897, *C. tripos* var. *arctica* Claparède *et* Lachmann 1859)
763 *Ceratium arietinum* Cleve 1900 (=*C. bucephalum* (Cleve 1897) Cleve 1901)
**Ceratium aultii* Graham *et* Bronikovsky 1944
**Ceratium axiale* Kofoid 1907 (=*C. axiale* (Kofoid) Karsten 1907)
764 *Ceratium azoricum* Cleve 1900

Tab. 1. – continued

**Ceratium balechii* Meave del Castillo, Okolodkov *et* Zamudio 2003 [intermediate with *Ceratium divaricatum/dens*] [Meave del Castillo *et al.* (2003)]

765 *Ceratium belone* Cleve 1900 (=*C. pacificum* Schröder 1906, non *C. pacificum* Wood 1963)

766 *Ceratium bigelowii* Kofoid 1907

767 *Ceratium breve* (Ostenfeld *et* Schmidt 1901) Schröder 1906 (=*C. tripos* var. *breve* Ostenfeld *et* Schmidt, *C. schmidtii* Jørgensen 1911, *C. curvicorne* Schmidt 1901)

**Ceratium brevearcuatum* Böhm 1976

768 *Ceratium brunellii* Rampi 1942 (=?*C. incisum* (Karsten 1905) Jørgensen 1911)

769 *Ceratium candelabrum* (Ehrenberg 1860) Stein 1883

770 *Ceratium carnegiei* Graham *et* Bronikowsky 1944

771 *Ceratium carriense* Gourret 1883 (=*C. massiliense* Pavillard 1907, *C. volans* Cleve 1900, *C. hundhausenii* Schröder 1906, non *C. volans* Pavillard 1905)

772 *Ceratium cephalotum* (Lemmermann 1900) Jørgensen 1911 (=*C. gravidum* var. *cephalotum* Lemmermann)

773 *Ceratium compressum* Gran 1912 (non *C. compressum* Gran 1902) [see Balech (1988: 141) for synonymy with *C. platycorne* Daday 1888]

774 *Ceratium concilians* Jørgensen 1920

775 *Ceratium contortum* (Gourret 1883) Cleve 1900 (=*C. contortum* var. *robustum* (Karsten 1907) Sournia 1966, *C. karstenii* f. *robustum* (Karsten) Jørgensen 1911, *C. karstenii* Pavillard 1927 partim, *C. longinum* (Karsten 1907) Jørgensen 1911, *C. saltans* Schröder 1906)

776 *Ceratium contrarium* (Gourret 1883) Pavillard 1905 (=*C. trichoceros* var. *contrarium* (Gourret) Schiller 1937)

777 *Ceratium declinatum* (Karsten 1907) Jørgensen 1911 (=*C. tripos declinatum* Karsten)

778 *Ceratium deflexum* (Kofoid 1907) Jørgensen 1911 (=*C. californiense* Karsten 1907, *C. recurvatum* Schröder 1906, *C. deflexum var. recurvatum* (Schröder) Jørgensen 1911)

779 *Ceratium dens* Ostenfeld *et* Schmidt 1901 (non *C. tripos* var. *ponticum*, non *C. divaricatum*) [see *C. divaricatum*]

780 *Ceratium digitatum* Schütt 1895

781 *Ceratium divaricatum* (Lemmermann 1900) Kofoid 1908 (=*C. tripos* var. *divaricatum* Lemmermann) [confused with *C. dens*]

**Ceratium egyptiacum* Halim 1963 (=?*C. tripos* var. *pulchellum* (Schröder 1906) López 1966 *ex* Sournia 1973)

**Ceratium ehrenbergii* Kofoid 1907 (=?*C. pentagonum* Gourret 1883)

782 *Ceratium euarcuatum* Jørgensen 1920 (=*C. arcuatum* Pavillard 1905, non *C. arcuatum* Cleve 1900)

783 *Ceratium extensum* (Gourret 1883) Cleve 1901 (=*C. strictum* Kofoid 1907, *C. biceps* Claparède *et* Lachmann 1859, *C. strictum* (Okamura *et* Nishikawa 1904) Kofoid 1907, *C. extensum* f. *strictum* Okamura *et* Nishikawa)

Tab. 1. – continued

784 *Ceratium falcatiforme* Jørgensen 1920 (=*C. inflatum falcatiforme* Peters 1934)
785 *Ceratium falcatum* (Kofoid 1907) Jørgensen 1920 (=*C. inflatum falcatum* Peters 1934)
**Ceratium filicorne* Steemann Nielsen 1934
786 *Ceratium furca* (Ehrenberg 1834) Claparède *et* Lachmann 1859 (=*C. biceps* Claparède *et* Lachmann 1859)
787 *Ceratium fusus* (Ehrenberg 1834) Dujardin 1841 (=*C. seta* (Ehrenberg 1859) Jørgensen 1911)
788 *Ceratium geniculatum* (Lemmermann 1900) Cleve 1911 (=*C. tricarinatum* Kofoid 1907)
789 *Ceratium gibberum* Gourret 1883
790 *Ceratium gravidum* Gourret 1883
791 *Ceratium hexacanthum* Gourret 1883 (=*C. reticulatum* (Pouchet 1883) Cleve 1903)
792 *Ceratium hircus* Schröder 1909 (=*C. furca* var. *hircus* (Schröder) Margalef 1961)
793 *Ceratium horridum* (Cleve 1897) Gran 1902 (=*C. tripos* var. *horridum* Cleve, *C. intermedium* (Jørgensen 1905) Jørgensen 1911, *C. claviger* Kofoid 1907, *C. tenue* (Ostenfeld *et* Schmidt 1901) Jørgensen 1911, *C. inclinatum* Kofoid 1907, *C. tenuissimum* Kofoid 1907, *C. mollis* Kofoid 1907, *C. batavum* Paulsen 1908, *C. leptosomum* Jørgensen 1911)
794 *Ceratium humile* Jørgensen 1911
795 *Ceratium incisum* (Karsten 1906) Jørgensen 1911 (=?*C. brunellii* Rampi 1942)
796 *Ceratium inflatum* (Kofoid 1907) Jørgensen 1911 (=*C. nipponicum* Okamura 1912, *C. pennatum* f. *inflata* Kofoid 1907)
797 *Ceratium karstenii* Pavillard 1907 (=*C. arcuatum* (Gourret 1883) Cleve 1900)
798 *Ceratium kofoidii* Jørgensen 1911 (=*C. boehmii* Graham *et* Bronikovsky 1944)
**Ceratium lanceolatum* Kofoid 1907
799 *Ceratium limulus* Gourret 1883 (=*C. tripos* var. *limulus* Gourret *in* Pouchet 1883)
800 *Ceratium lineatum* (Ehrenberg 1854) Cleve 1899
801 *Ceratium longipes* (Bailey 1850) Gran 1902
802 *Ceratium longirostrum* Gourret 1883 (=*C. scapiforme* Kofoid 1907, *C. pennatum* var. *scapiforme* (Kofoid) Jørgensen 1911)
803 *Ceratium longissimum* (Schröder 1900) Kofoid 1907
804 *Ceratium lunula* (Schimper *ex* Karsten 1905) Jørgensen 1911 (=*C. tripos lunula* Schimper *in* Karsten, *C. arcuatum* Okamura *et* Nishikawa 1904)
805 *Ceratium macroceros* (Ehrenberg 1840) Vanhöffen 1897 (=*C. californiense* Kofoid 1907)
806 *Ceratium massiliense* (Gourret 1883) Jørgensen 1911 (=*C. ostenfeldii* Kofoid 1907, *C. protuberans* (Karsten 1905) Paulsen 1930, *C. undulatum* Schröder 1906)
807 *Ceratium minutum* Jørgensen 1920

Tab. 1. – continued

**Ceratium pacificum* Wood 1963 (non *C. pacificum* Schröder 1906)

808 *Ceratium paradoxides* Cleve 1900

809 *Ceratium pavillardii* Jørgensen 1911 (=*C. vultur* Pavillard 1905, non *C. vultur* Cleve 1900)

810 *Ceratium pentagonum* Gourret 1883 (=*C. subrobustum* (Jørgensen) Steemann Nielsen 1934)

811 *Ceratium petersii* Steemann Nielsen 1934

812 *Ceratium platycorne* Daday 1888 (=*C. lamellicorne* Kofoid 1908) [see Balech (1988: 141) for synonymy with *C. compressum* Gran 1902/1912)]

813 *Ceratium praeolongum* (Lemmermann 1900) Kofoid 1907 *ex* Jørgensen 1911 (=*C. gravidum* var. *praelongum* Lemmermann)

814 *Ceratium pulchellum* Schröder 1906

**Ceratium ramakrishnii* Subrahmanyan 1968 (=?*C. trichoceros* (Ehrenberg 1860) Kofoid 1908)

815 *Ceratium ranipes* Cleve 1900 (=*C. palmatum* (Schröder 1901) Schröder 1906)

816 *Ceratium reflexum* Cleve 1900

817 *Ceratium schrankii* Kofoid 1907

818 *Ceratium schroeteri* Schröder 1906

819 *Ceratium setaceum* Jørgensen 1911

820 *Ceratium symmetricum* Pavillard 1905 (=*C. coarctatum* Pavillard 1905, *C. gracile* (Gourret 1883) Jørgensen 1911)

**Ceratium tasmaniae* Wood 1963

821 *Ceratium teres* Kofoid 1907

822 *Ceratium trichoceros* (Ehrenberg 1860) Kofoid 1908 (=*C. flagelliferum* Cleve 1900)

823 *Ceratium tripos* (O.F. Müller 1777) Nitzsch 1817 (=*C. schroederi* Nie 1936, *C. neglectum* Ostenfeld 1903, *C. tripodioides* (Jørgensen 1920) Steemann Nielsen 1934)

**Ceratium uncinus* Sournia 1972

**Ceratium uteri* A.S. Campbell 1934

824 *Ceratium vultur* Cleve 1900 (=*C. sumatranum* (Karsten 1907) Jørgensen 1911, *C. recurvum* (Jørgensen) Reinecke 1973, non *C. vultur* Pavillard 1905, *C. japonicum* Schröder 1906, *C. vultur* f. *japonicum* (Schröder) Wood 1955)

Ceratocorythaceae Lindemann 1928

54 *Ceratocorys* Stein 1883 (12 species)

825 *Ceratocorys anacantha* Carbonell-Moore 1996 [Carbonell-Moore (1996a)]

826 *Ceratocorys armata* (Schütt 1895) Kofoid 1910 (=*C. spinifera* Murray *et* Whitting 1899, *Goniodoma fimbriatum* Murray *et* Whitting 1899)

Tab. 1. – continued

827 *Ceratocorys aultii* Graham 1942
828 *Ceratocorys bipes* (Cleve 1903) Kofoid 1910 (=*C. asymmetrica* Karsten 1907)
829 *Ceratocorys gourretii* Paulsen 1931 (=*C. allenii* Osorio-Tafall 1942, *Phalacroma jourdanii* (Gourret 1883) Schütt 1895)
830 *Ceratocorys grahamii* Carbonell-Moore 1996 [Carbonell-Moore (1996a)]
831 *Ceratocorys horrida* Stein 1883 (=*C. hirsuta* Matzenauer 1933, *Dinophysis jourdanii* Gourret 1883)
832 *Ceratocorys indica* Wood 1963
833 *Ceratocorys kofoidii* Paulsen 1931 [probably *C. gourretii* Paulsen 1931]
834 *Ceratocorys magna* Kofoid 1910 (=*C. spinifera* Murray *et* Whitting 1899 partim)
835 *Ceratocorys reticulata* Graham 1942 [resembles *C. armata* (Schütt 1895) Kofoid 1910]
836 *Ceratocorys skogsbergii* Graham 1942

Cladopyxidaceae Poche 1913

Cladopyxidaceae Stein 1883 emend. Balech 1967

55 ***Cladopyxis*** Stein 1883 (=***Micracanthodinium*** Deflandre 1937 partim)
837 *Cladopyxis brachiolata* Stein 1883 (=*C. spinosa* (Kofoid 1907) Schiller 1937, *C. steinii* Zacharias 1906)
838 *Cladopyxis caryophyllum* (Kofoid 1907) Pavillard 1931 (=*Acanthodinium caryophyllum* Kofoid)
839 *Cladopyxis hemibranchiata* Balech 1964
Cladopyxis quadrispina Pavillard 1931 (=*Micracanthodinium quadrispinum* (Pavillard) Margalef 1969)
56 ***Micracanthodinium*** Deflandre 1937 (=***Cladopyxis*** Stein 1883 partim) [thecal plates not reported]
840 *Micracanthodinium bacilliferum* (Schiller 1937) Deflandre 1937 (=*C. bacillifera* Schiller)
841 *Micracanthodinium claytonii* (R.W. Holmes 1956) Dodge 1982 (=*C. claytonii* R.W. Holmes)
842 *Micracanthodinium setiferum* (Lohmann 1902) Deflandre 1937 (=*C. setifera* Lohmann)
57 ***Palaeophalacroma*** Schiller 1928
843 *Palaeophalacroma connectens* (Nie 1945) Loeblich III 1980 (=*Sinodinium connectens* Nie)
844 *Palaeophalacroma unicinctum* Schiller 1928 (=*Heterodinium detonii* Rampi 1943, *Epiperidinium michaelsarsii* Gaarder 1954)
845 *Palaeophalacroma sphaericum* F.J.R. Taylor 1976
846 *Palaeophalacroma verrucosum* Schiller 1928
58 ***Peridiniella*** Kofoid *et* Michener 1911 emend. Balech 1977
847 *Peridiniella catenata* (Levander 1894) Balech 1977 (=*Gonyaulax catenata* (Levander) Kofoid 1911, *Peridinium catenatum* Levander, *Amylax catenata* Meunier 1910)

Tab. 1. – continued

848 *Peridiniella danica* (Paulsen 1907) Okolodkov *et* Dogde 1995 (=*Glenodinium danicum* Paulsen 1907 *ex* Braarud 1935 partim) [Okolodkov and Dogde (1995)]

849 *Peridiniella sphaeroidea* Kofoid *et* Michener 1911

Crypthecodiniaceae Biecheler *ex* Chatton 1952

59 *Crypthecodinium* Biecheler 1938

850 *Crypthecodinium cohnii* (Seligo 1886) Chatton *in* Grassé 1952 (=*Glenodinium cohnii* Seligo *in* Cohn 1887, *Gyrodinium cohnii* (Seligo) Schiller 1933, *C. setense* Biecheler 1938, *Gymnodinium fucorum* Küster 1908, *Gyrodinium fucorum* (Küster) Kofoid *et* Swezy 1921)

Goniodomataceae Lindemann 1928

60 *Gambierdiscus* Adachi *et* Fukuyo 1979 (6 species)

851 *Gambierdiscus australes* Chinain *et* Faust 1999 [Chinain *et al.* (1999)] (A suffix is lacking in the epithet, »australesanus« or »australesensis«)

852 *Gambierdiscus belizeanus* Faust 1995 [Faust (1995)] (the epithet »belizianus« is orthographically correct, ICBN Art. 60.1)

853 *Gambierdiscus pacificus* Chinain *et* Faust 1999 [Chinain *et al.* (1999)]

854 *Gambierdiscus polynesiensis* Chinain *et* Faust 1999 [Chinain *et al.* (1999)]

855 *Gambierdiscus toxicus* Adachi *et* Fukuyo 1979

856 *Gambierdiscus yasumotoi* M.J. Holmes 1998 [Holmes (1998)]

61 *Goniodoma* Stein 1883 (=***Triadinium*** Dodge 1981, ***Heteraulacus*** Diesing 1850 partim)

857 *Goniodoma acuminatum* (Ehrenberg 1838) Stein 1883 (=*Peridinium acuminatum* Ehrenberg, non *Peridinium polyedricum* Pouchet 1883)
**Goniodoma crassum* Kofoid *et* Michener 1911

858 *Goniodoma polyedricum* (Pouchet 1883) Jørgensen 1899 (=*Peridinium polyedricum* Pouchet, *Triadinium polyedricum* (Pouchet) Dodge 1981, *Goniodoma acuminata* Stein 1883 partim, non *Peridinium acuminatum* Ehrenberg 1838)

859 *Goniodoma sphaericum* Murray *et* Whitting 1899 (=*Triadinium sphaericum* (Murray *et* Whitting) Dodge 1981, *Heteraulacus sphaericum* (Murray *et* Whitting) Loeblich III 1970)

62 *Pyrodinium* Plate 1906

860 *Pyrodinium bahamense* Plate 1906 (=*P. bahamense* Plate 1906 var. *bahamense*/ var. *compressum* (Böhm 1931) Steidinger, Tester *et* F.J.R. Taylor 1980,
P. bahamense f. *compressa* Böhm 1931, *P. schilleri* (Matzenauer 1933) Schiller 1935, *Gonyaulax schilleri* Matzenauer 1933)
**Pyrodinium phoneus* Woloszyńska *et* Conrad 1939 (=*Gonyaulax phoenus* (Woloszyńska *et* Conrad) F.J.R. Taylor 1975, =*?Alexandrium ostenfeldii* (Paulsen) Balech *et* Tangen, *Gonyaulax phoneus* (Woloszyńska *et* Conrad) Loeblich Jr. *et* Loeblich III 1975)

Tab. 1. – continued

	Gonyaulacaceae Lindemann 1928
63	***Alexandrium*** Halim emend. Balech 1989 (=***Gonyaulax*** Diesing 1866 partim, ***Protogonyaulax*** F.J.R. Taylor 1976, ***Gessnerium*** Halim 1967 *ex* Halim 1969, ***Goniodoma*** Stein 1883 partim) (28 species)
861	*Alexandrium acatenella* (Whedon *et* Kofoid 1936) Balech 1985 (=*G. acatenella* Whedon *et* Kofoid, *Protogonyaulax acatenella* (Whedon *et* Kofoid) F.J.R. Taylor 1979)
862	*Alexandrium affine* (Inoue *et* Fukuyo 1985) Balech 1985 (=*A. fukuyoi* Balech 1985, *Protogonyaulax affinis* Inoue *et* Fukuyo) [related to *A. concavum*]
863	*Alexandrium andersonii* Balech 1990
864	*Alexandrium balechii* (Steidinger 1971) Balech 1995 (=*G. balechii* Steidinger) [Balech (1995)]
865	*Alexandrium camurascutulum* MacKenzie *et* Todd 2002 [MacKenzie and Todd (2002)]
866	*Alexandrium catenella* (Whedon *et* Kofoid 1936) Balech 1985 (=*G. catenella* Whedon *et* Kofoid 1936, *G. washingtonensis* Hsu 1967)
867	*Alexandrium cohorticula* (Balech 1967) Balech 1985 (=*G. cohorticula* Balech)
868	*Alexandrium compressum* (Fukuyo, Yoshida *et* Inoue 1985) Balech 1995 (=*Protogonyaulax compressa* Fukuyo, Yoshida *et* Inoue) [Balech (1995)]
869	*Alexandrium concavum* (Gaarder 1942) Balech 1985 (=*Goniodoma concavum* Gaarder, *Gonyaulax concava* sensu Balech 1967) [related to *A. affine*]
870	*Alexandrium depressum* (Gaarder 1954) Balech *et* Tangen 1985 (=*Goniodoma depressum* Gaarder, *Gonyaulax depressum* (Gaarder) Balech 1979)
871	*Alexandrium foedum* Balech 1990
872	*Alexandrium fraterculus* (Balech 1964) Balech 1985 (=*G. fratercula* Balech)
873	*Alexandrium fundyense* Balech 1985 (=*G. excavata* (Braarud 1945) Balech 1971 sensu L.A. Loeblich *et* Loeblich III 1975, non Balech 1971)
874	*Alexandrium hiranoi* Kita *et* Fukuyo 1988 (=*Goniodoma pseudogoniaulax* Biecheler sensu Kita *et al.* 1985)
875	*Alexandrium insuetum* Balech 1985
876	*Alexandrium kutnerae* (Balech 1979) Balech 1985 (=*G. kutnerae* Balech)
877	*Alexandrium leei* Balech 1985
878	*Alexandrium margalefii* Balech 1994 [Balech (1994b)]
879	*Alexandrium minutum* Halim 1960 (=*A. ibericum* Balech 1985, *A. lusitanicum* Balech 1985, *A. angustitabulatum* F.J.R.Taylor *in* Balech 1995)
880	*Alexandrium monilatum* (Howell 1953) Balech 1985 (=*G. monilata* Howell, *Gessnerium mochimaensis* Halim 1967 *ex* Halim 1969)
881	*Alexandrium ostenfeldii* (Paulsen 1904) Balech *et* Tangen 1985 (=*Goniodoma ostenfeldii* Paulsen, *Gonyaulax ostenfeldii* (Paulsen) Paulsen 1949, *Protogonyaulax ostenfeldii* (Paulsen) Fraga *et* Sánchez 1985, *Heteraulacus ostenfeldii* (Paulsen) Loeblich III 1970, *Gessnerium ostenfeldii* (Paulsen) Loeblich III *et* L.A. Loeblich,

Tab. 1. – continued

Triadinium ostenfeldii (Paulsen) Dodge *in* Parke *et* Dodge 1976, *G. globosa* (Braarud 1945) Balech, *Protogonyaulax globosa* (Braarud) F.J.R. Taylor 1976,?*Gonyaulax trygvei* Dodge *in* Parke *et* Dodge 1976)

882 *Alexandrium peruvianum* (Balech *et* Mendiola 1977) Balech *et* Tangen 1985 (=*G. peruviana* Balech *et* Mendiola)

883 *Alexandrium pseudogoniaulax* (Biecheler 1952) Horiguchi 1983 *ex* Kita *et* Fukuyo 1992 (=*Goniodoma pseudogoniaulax* Biecheler, non »pseudogonyaulax«)

884 *Alexandrium satoanum* Yuki *et* Fukuyo 1992 (For the epithets commemorating persons, substantive epithets »satoi« are more commonly applied than adjectival epithets, ICBN Art. 60.11)

885 *Alexandrium tamarense* (Lebour 1925) Balech 1985 (=*G. tamarensis* Lebour, *A. excavatum* (Braarud 1945) Balech *et* Tangen 1985)

886 *Alexandrium tamiyavanichii* Balech 1994 (=*A. cohorticula* (Balech 1967) Balech 1985 sensu Ogata *et al.* 1990, non Balech 1985, *Protogonyaulax cohorticula* (Balech) F.J.R. Taylor 1979) [Balech (1994b)]

887 *Alexandrium taylorii* Balech 1994 [Balech (1994b)]

888 *Alexandrium tropicale* Balech 1985 (=*Gonyaulax excavata* (Braarud 1945) Balech 1971)

64 ***Amylax*** Meunier 1910 (=***Gonyaulax*** Diesing 1866 partim)

889 *Amylax buxus* (Balech 1967) Dodge 1989 (=*Gonyaulax buxus* Balech)

890 *Amylax triacantha* (Jørgensen 1899) Sournia 1984 (=*G. triacantha* Jørgensen, *G. hyperborea* (Cleve 1900) Paulsen 1903, *Amylax lata* Meunier 1910)

**Amylax verrucosa* Rampi 1943

65 ***Gonyaulax*** Diesing 1866 (=***Amylax*** Meunier 1910 partim) [taxonomic junior of *Spiniferites* Mantell 1850] (60 species)

891 *Gonyaulax acuta* Kofoid *et* Michener 1911 (=?*G. birostris* Stein 1883)

892 *Gonyaulax africana* Schiller 1929

893 *Gonyaulax alaskensis* Kofoid 1911

894 *Gonyaulax apiculata* (Pénard 1891) Entz 1904 (=*G. apiculata* var. *clevei* Ostenfeld 1908)

895 *Gonyaulax areolata* Kofoid *et* Michener 1911

896 *Gonyaulax baltica* Ellegaard, J. Lewis *et* Harding 2002 [Ellegaard *et al.* (2002)]

897 *Gonyaulax birostris* Stein 1883 (=*G. glyptorhynchus* Murray *et* Whitting 1899, *G. highlei* Murray *et* Whitting 1899)

**Gonyaulax bispinosa* Kofoid *et* Michener 1911

898 *Gonyaulax borealis* Nordli 1951

899 *Gonyaulax braarudii* Hasle 1960

900 *Gonyaulax brevisulcata* P. Dangeard 1927 (=*G. paulsenii* Gaarder 1954)

Tab. 1. – continued

901	*Gonyaulax bruunii* F.J.R. Taylor 1976 [close to *G. taylorii* Carbonell-Moore 1996]
902	*Gonyaulax ceratocoroides* Kofoid 1910 (=*Ceratocorys spinifera* Murray *et* Whitting 1899, *Acanthogonyaulax spinifera* (Murray *et* Whitting) Graham 1942)
903	*Gonyaulax cochlea* Meunier 1919
	**Gonyaulax conjuncta* Wood 1954
	**Gonyaulax dangeardii* (P. Dangeard 1927) Schiller 1935 (=*G. pavillardii* P. Dangeard 1927, non *G. pavillardii* Kofoid *et* Michener 1911)
904	*Gonyaulax diegensis* Kofoid 1911
905	*Gonyaulax digitalis* (Pouchet 1883) Kofoid 1911 (=*Protoperidinium digitale* Pouchet, *Peridinium digitale* Lemmermann 1899)
906	*Gonyaulax dimorpha* Biecheler 1952 [resembles *Alexandrium peruvianus* (Balech *et* Mendiola 1977) Balech *et* Tangen 1985]
907	*Gonyaulax elegans* Rampi 1951
908	*Gonyaulax elongata* (Reid 1974) Ellegaard, Daugbjerg, Rochon, J. Lewis *et* Harding 2003 (=*Spiniferites elongatus* Reid) [Ellegaard *et al.* (2003)]
909	*Gonyaulax expansa* Kofoid *et* Michener 1911 [probably *G. birostris* Stein 1883]
910	*Gonyaulax fragilis* (Schütt 1895) Kofoid 1911 (=*Steiniella fragilis* Schütt)
911	*Gonyaulax fusiformis* Graham 1942 (non *G. birostris* Stein 1883, non *G. jolliffei* Murray *et* Whitting 1899)
912	*Gonyaulax globosa* (Braarud 1945) Balech 1971 (=*G. tamarensis* Lebour var. *globosa* Braarud,?*G. trygvei* Parke *in* Parke *et* Dodge 1976)
	**Gonyaulax grabrielae* Schiller 1935
913	*Gonyaulax gracilis* Schiller 1935
914	*Gonyaulax helensis* Woloszyńska 1928
915	*Gonyaulax hyalina* Ostenfeld *et* Schmidt 1901
	**Gonyaulax inclinata* Kofoid *et* Michener 1911
916	*Gonyaulax inflata* (Kofoid 1907) Kofoid 1911 (=*G. pavillardii* P. Dangeard 1927, non *G. pavillardii* (P. Dangeard) Schiller 1935)
917	*Gonyaulax kofoidii* Pavillard 1909 [related to *G. pacifica* Kofoid 1907]
918	*Gonyaulax lebourae* Balech 1979 (=*G. orientalis* Lindemann 1924 sec Lebour 1925, non *G. orientalis* Lindemann, *Goniodoma orientale* (Lindemann) Balech 1979)
919	*Gonyaulax ligustica* Rampi 1951
	**Gonyaulax loculata* Meunier 1919
	**Gonyaulax longicornu* P.H. Campbell 1973
920	*Gonyaulax macroporus* Mangin 1922

Tab. 1. – continued

Gonyaulax matkovichii Schiller 1929

921 *Gonyaulax membranacea* (Rossignol 1964) Ellegaard, Daugbjerg, Rochon, J. Lewis *et* Harding 2003 (=*Hystrichosphaera furcata* var. *membranacea* Rossignol) [Ellegaard *et al.* (2003)]

922 *Gonyaulax milneri* (Murray *et* Whitting 1899) Kofoid 1911

923 *Gonyaulax minuta* Kofoid *et* Michener 1911 (=*G. minima* Matzenauer 1933)

924 *Gonyaulax monacantha* Pavillard 1916

925 *Gonyaulax monospina* Rampi 1951

926 *Gonyaulax nigricans* (Schiller 1937) Balech 1988 (=*Melanodinium nigricans* Schiller)

927 *Gonyaulax nivicola* (Meunier 1910) Kofoid 1911

928 *Gonyaulax obliqua* Lemmermann 1899

929 *Gonyaulax orientalis* Lindemann 1924 (=*Goniodoma orientale* (Lindemann) Balech 1979, *Triadinium orientale* (Lindemann) Dodge 1981, *G. lebourae* Balech 1980 partim, non *G. orientalis* sensu Lebour 1925)

930 *Gonyaulax ovalis* Schiller 1929 (=?*G. ovata* Matzenauer 1933)

931 *Gonyaulax ovata* Matzenauer 1933

932 *Gonyaulax parva* Ramsfjell 1959

933 *Gonyaulax pacifica* Kofoid 1907 (=*Steiniella cornuta* Karsten 1907, *Pavillardinium brianii* (Rampi 1941) Sournia 1973,?*G. kofoidii* Pavillard 1909]

Gonyaulax paucula Kofoid *et* Michener 1911

934 *Gonyaulax pavillardii* Kofoid *et* Michener 1911 (non *G. pavillardii* P. Dangeard 1927)

935 *Gonyaulax perpusilla* (Meunier 1910) Kofoid 1911

936 *Gonyaulax polygramma* Stein 1883 (=*G. schuettii* Lemmermann 1899, non *Gonyaulax polygramma* Meunier 1910)

937 *Gonyaulax reticulata* Kofoid *et* Michener 1911 (=*G. polygramma* sensu F.J.R. Taylor 1962)

938 *Gonyaulax rostratum* P. Dangeard 1927, "? rostrata"

939 *Gonyaulax rotundata* Rampi 1951

Gonyaulax rugosa Wailes 1928

940 *Gonyaulax scrippsae* Kofoid 1911

Gonyaulax senta Kofoid *et* Michener 1911

941 *Gonyaulax sousae* Balech 1959

942 *Gonyaulax subulata* Kofoid *et* Michener 1911 (non *G. subulata* sensu F.J.R. Taylor 1976)

Tab. 1. – continued

943 *Gonyaulax sphaeroidea* Kofoid 1911 (=*G. globosum* Schiller 1929)
944 *Gonyaulax spinifera* (Claparède *et* Lachmann 1859) Diesing 1866 (=*G. levanderi* (Lemmermann) Paulsen 1907, non *G. spinifera* Stein 1883)
945 *Gonyaulax striata* Mangin 1922
946 *Gonyaulax taylorii* Carbonell-Moore 1996 (=*G. monacantha* var. *minor* sensu Balech 1971) [Carbonell-Moore (1996b)]
947 *Gonyaulax trottii* Rampi 1951
948 *Gonyaulax turbynei* Murray *et* Whitting 1899
949 *Gonyaulax unicornis* Lebour 1925
950 *Gonyaulax verior* Sournia 1973 (=*Amylax diacantha* Meunier 1919, *G. diacantha* sensu Schiller 1937, *G. longispina* Lebour 1925)
66 ***Lingulodinium*** Wall 1967 emend. Dodge 1989
951 *Lingulodinium milneri* (Murray *et* Whitting 1899) Dodge 1989 (=*Gonyaulax milneri* (Murray *et* Whitting) Kofoid 1911)
952 *Lingulodinium polyedra* (Stein 1883) Dodge 1989 (=*Gonyaulax polyedra* Stein 1883) [reported frequently as »polyedrum«]
67 ***Protoceratium*** Bergh 1881 (=***Gonyaulax*** Diesing 1866 partim)
**Protoceratium aculeatum* (Stein 1883) Schiller 1937 (=*Clathrocysta aculeata* Stein)
953 *Protoceratium areolatum* Kofoid 1907
**Protoceratium cancellorum* Kofoid *et* Michener 1911
**Protoceratium globosum* Kofoid *et* Michener 1911
954 *Protoceratium pepo* Kofoid *et* Michener 1911
**Protoceratium promissum* Kofoid *et* Michener 1911
955 *Protoceratium reticulatum* (Claparède *et* Lachmann 1859) Bütschli 1885 (=*G. grindleyi* Reinecke 1967, *Protoceratium aceros* Bergh 1881, *Peridiniopsis reticulata* (Claparède *et* Lachmann) Starmach 1974)
956 *Protoceratium spinulosum* (Murray *et* Whitting 1899) Schiller 1937
**Protoceratium splendens* Meunier 1910 (=?*P. reticulatum* (Claparède *et* Lachmann 1859) Bütschli 1885)

Heterocapsaceae Fensome *et al.* 1993

68 ***Heterocapsa*** Stein 1883 emend. Iwataki *et* Fukuyo 2002 (=***Cachonina*** Loeblich III 1968) [Iwataki (2002)] (12 species)
957 *Heterocapsa arctica* Horiguchi 1997 [Horiguchi (1997)]
**Heterocapsa chattonii* (Biecheler 1952) P.H. Campbell 1973 (=*Peridinium chattonii* Biecheler)
958 *Heterocapsa circularisquama* Horiguchi 1995 [Horiguchi (1995b)]
959 *Heterocapsa illdefina* (Herman *et* Sweeney 1976) Morrill *et* Loeblich III 1981 (=*Cachonina illdefina* Herman *et* Sweeney)

Tab. 1. – continued

960 *Heterocapsa horiguchii* Iwataki, Takayama *et* Matsuoka 2002 [Iwataki *et al.* (2002)]
961 *Heterocapsa lanceolata* Iwataki *et* Fukuyo 2002 [Iwataki *et al.* (2002)]
**Heterocapsa kollmeriana* M.J. Swift *et* McLaughlin 1970 [freshwater]
962 *Heterocapsa minima* Pomroy 1989
963 *Heterocapsa niei* (Loeblich III 1968) Morrill *et* Loeblich III 1981
964 *Heterocapsa orientalis* Iwataki *et* Fukuyo 2003 [Iwataki *et al.* (2003)]
965 *Heterocapsa ovata* Iwataki *et* Fukuyo 2003 [Iwataki *et al.* (2003)]
**Heterocapsa pacifica* Kofoid 1907
**Heterocapsa pseudotriquetra* Iwataki, G. Hansen *et* Fukuyo 2002 [described in a PhD, Iwataki (2002)]
966 *Heterocapsa pygmaea* Loeblich III, R.J. Schmidt *et* Sherley 1981 (=*Cachonina pygmaea* (Loeblich III, R.J. Schmidt *et* Sherley 1981) Sournia 1984)
**Heterocapsa quinquecuspidata* Massart 1920 (=?*Peridiniopsis cunningtonii* Lemmermann 1907)
967 *Heterocapsa rotundata* (Lohmann 1908) G. Hansen 1995 (=*Amphidinium rotundatum* Lohmann 1911, *A. pellucidum* Redeke 1935, *Gymnodinium minutum* Lebour 1925, *Massartia rotundata* (Lohmann) Schiller 1933, *Katodinium rotundatum* (Lohmann) Loeblich III 1965, *Katodinium redekei* (Conrad *et* Kufferath 1954) Loeblich III 1965, *Katodinium minutum* (Lebour) Sournia 1973) [Hansen (1995)]
968 *Heterocapsa triquetra* (Ehrenberg 1840) Stein 1883 (=*Glenodinium triquetrum* Ehrenberg, *Peridinium triquetrum* (Ehrenberg) Lebour 1925, *Properidinium heterocapsa* (Stein) Meunier 1919)
**Heterocapsa umbilicata* Stein 1883

Heterodiniaceae Lindemann 1928

69 ***Heterodinium*** Kofoid 1906 (=***Peridinium*** Ehrenberg 1830 partim) (42 species)
969 *Heterodinium agassizii* Kofoid 1907
970 *Heterodinium angulatum* Kofoid *et* Michener 1911
971 *Heterodinium asymmetricum* Kofoid *et* Adamson 1933
972 *Heterodinium australiae* Wood 1963
973 *Heterodinium balechii* Rampi 1951
974 *Heterodinium blackmanii* (Murray *et* Whitting 1899) Kofoid 1906 (=*H. curvatum* Kofoid 1907)
**Heterodinium calvum* Kofoid 1907
975 *Heterodinium crassipes* Schiller 1916

Tab. 1. – continued

976 *Heterodinium debeauxii* Rampi 1941
977 *Heterodinium deformatum* (Kofoid 1907) Kofoid *et* Adamson 1933 (=*H. gesticulatum* f. *deformata* Kofoid 1907)
978 *Heterodinium dispar* Kofoid *et* Adamson 1933
979 *Heterodinium donna* (Murray *et* Whitting 1899) Kofoid 1906
980 *Heterodinium dubium* Rampi 1941
981 *Heterodinium elongatum* Kofoid *et* Michener 1911
982 *Heterodinium expansum* Kofoid 1907
983 *Heterodinium extremum* (Kofoid 1907) Kofoid *et* Adamson 1933 (=*H. gesticulatum* f. *extrema* Kofoid 1907)
984 *Heterodinium fenestratum* Kofoid 1907
985 *Heterodinium fides* Kofoid 1907
986 *Heterodinium gesticulatum* Kofoid 1907 (=*Peridinium tristylum* Hensen 1911)
987 *Heterodinium globosum* Kofoid 1907 (=?*H. gracile* Böhm 1936)
988 *Heterodinium gracile* Böhm 1936 (=?*H. globosum* Kofoid 1907)
989 *Heterodinium grahamii* Rampi 1941
990 *Heterodinium hindmarchii* (Murray *et* Whitting 1899) Kofoid 1906
991 *Heterodinium inaequale* (Kofoid 1906) Schiller 1937 (=*H. laticinctum* Kofoid 1907, *H. kofoidii* Pavillard 1915)
992 *Heterodinium kofoidii* Pavillard 1915 (=*H. pavillardii* Kofoid *et* Adamson 1933, non *H. kofoidii* Schiller 1916=*H. schilleri* Pavillard 1932)
**Heterodinium laeve* Kofoid *et* Michener 1911
993 *Heterodinium laticeps* Léger 1972
994 *Heterodinium leiorhynchum* (Murray *et* Whitting 1899) Kofoid 1906
**Heterodinium lineatum* Kofoid *et* Michener 1911 (=*Dolichodinium lineatum* (Kofoid *et* Michener) Kofoid *et* Adamson 1933)
995 *Heterodinium mediocre* (Kofoid 1907) Kofoid *et* Adamson 1933 (=*H. gesticulatum* f. *mediocris* Kofoid, ?*H. sinistrum* Kofoid *et* Adamson 1933)
996 *Heterodinium mediterraneum* Pavillard 1932
997 *Heterodinium milneri* (Murray *et* Whitting 1899) Kofoid 1906
998 *Heterodinium minutum* Kofoid *et* Michener 1911
999 *Heterodinium murrayi* Kofoid 1906 (=*Peridinium tripos* Murray *et* Whitting 1899)
1000 *Heterodinium obesum* Kofoid 1907
**Heterodinium praetextum* Kofoid 1907

Tab. 1. – continued

1001 *Heterodinium rigdenae* Kofoid 1906 (=*H. longum* Kofoid 1907)
1002 *Heterodinium schilleri* Pavillard 1932 (=*H. kofoidii* Schiller 1916, non *H. kofoidii* Pavillard 1915=*H. pavillardii* Kofoid *et* Adamson 1933)
1003 *Heterodinium scottii* Kofoid *et* Adamson 1933
1004 *Heterodinium scrippsii* Kofoid 1906 (=*H. richardii* Pavillard 1932, *H. pulchrum* Böhm 1933, *Peridinium areolatum* Karsten 1906)
1005 *Heterodinium sinistrum* Kofoid *et* Adamson 1933 (=*H. sinistrum* f. *sinistrum* (Kofoid *et* Adamson 1933) Schiller 1936)
1006 *Heterodinium sphaeroideum* Kofoid 1906
**Heterodinium spiniferum* Kofoid *et* Michener 1911
1007 *Heterodinium superbum* Kofoid 1907
1008 *Heterodinium trirostre* (Murray *et* Whitting 1899) Kofoid 1906
1009 *Heterodinium varicator* Kofoid *et* Adamson 1933
1010 *Heterodinium whittingae* Kofoid 1906

Ostreopsidaceae Lindemann 1928

70 ***Coolia*** Meunier 1919 (=***Ostreopsis*** Schmidt 1901 partim)
1011 *Coolia areolata* Ten-Hage, Turquet, Quod *et* Couté 2000 [Ten-Hage *et al.* (2000a)]
1012 *Coolia monotis* Meunier 1919 (=*Ostreopsis monotis* (Meunier) Lindemann 1928, *Glenodinium monotis* (Meunier) Biecheler 1952)
1013 *Coolia tropicalis* Faust 1995 [Faust (1995)]
71 ***Ostreopsis*** Schmidt 1901
1014 *Ostreopsis belizeana* Faust 1999 [Faust (1999)] (published as »belizeanum«, ICBN Art. 23.5 and 32.5; »beliziana« is orthographically correct, ICBN Art. 60.1)
1015 *Ostreopsis caribbeana* Faust 1999 [Faust (1999)]
(published as »caribbeanus«, ICBN Art. 23.5 and 32.5; »caribeana« is orthographically correct, ICBN Art. 60.1)
1016 *Ostreopsis heptagona* Norris, Bomber *et* Balech 1985
1017 *Ostreopsis labens* Faust *et* Morton 1995 [Faust and Morton (1995)]
1018 *Ostreopsis lenticularis* Fukuyo 1981
1019 *Ostreopsis marina* Faust 1999 [Faust (1999)] (published as »marinus«, ICBN Art. 23.5 and 32.5)
1020 *Ostreopsis mascarenensis* Quod 1994 [Quod (1994)]
1021 *Ostreopsis ovata* Fukuyo 1981
1022 *Ostreopsis siamensis* Schmidt 1901

Tab. 1. – continued

Oxytoxaceae Lindemann 1928

72 ***Amphidiniopsis*** Woloszyńska 1929 (=***Thecadinium*** Kofoid *et* Skogsberg 1928 partim) (11 species)

1023 *Amphidiniopsis arenaria* Hoppenrath 2000 [Hoppenrath (2000e)]

1024 *Amphidiniopsis cristata* Hoppenrath 2000 [Hoppenrath (2000e)]

1025 *Amphidiniopsis dentata* Hoppenrath 2000 [Hoppenrath (2000e)]

1026 *Amphidiniopsis galericulata* Hoppenrath 2000 [Hoppenrath (2000e)]

1027 *Amphidiniopsis hexagona* Yoshimatsu, Toriumi *et* Dodge 2000 [Yoshimatsu *et al.* (2000)]

1028 *Amphidiniopsis hirsuta* (Balech 1956) Dodge 1982 (=*Thecadinium hirsutum* Balech)

1029 *Amphidiniopsis kofoidii* Woloszyńska 1929 (non *Thecadinium kofoidii* (Herdman 1923) J. Larsen 1985)

1030 *Amphidiniopsis korewalensis* S. Murray *et* Patterson 2002 [Murray and Patterson (2002)]

1031 *Amphidiniopsis pectinaria* Toriumi, Yoshimatsu *et* Dodge 2002 [Toriumi *et al.* (2002)]

1032 *Amphidiniopsis swedmarkii* (Balech 1956) Dodge 1982 (=*Thecadinium swedmarkii* Balech)

**Amphidiniopsis urnaeformis* Gail 1950 (=?*Spatulodinium pseudonoctiluca*)

1033 *Amphidiniopsis uroensis* Toriumi, Yoshimatsu *et* Dodge 2002 [Toriumi *et al.* (2002)]

73 ***Centrodinium*** Kofoid 1907 (=***Pavillardinium*** De-Toni 1936 partim, ***Murrayella*** Kofoid 1907 partim) (14 species)

1034 *Centrodinium biconicum* (Murray *et* Whitting 1899) F.J.R. Taylor 1976 (=*M. biconica* (Murray *et* Whitting) Pavillard 1931, *Pavillardinium biconicum* Rampi 1948)

1035 *Centrodinium complanatum* (Cleve 1903) Kofoid 1907 (=*Steiniella complanata* Cleve)

1036 *Centrodinium deflexum* Kofoid 1907

1037 *Centrodinium deflexoides* Balech 1962

1038 *Centrodinium elongatum* Kofoid 1907

1039 *Centrodinium eminens* Böhm 1933

**Centrodinium expansum* Kofoid 1911

1040 *Centrodinium intermedium* Pavillard 1930

1041 *Centrodinium maximum* Pavillard 1930

1042 *Centrodinium mimeticum* (Balech 1967) F.J.R. Taylor 1976 (=*M. mimetica* Balech)

1043 *Centrodinium pacificum* (Rampi 1950) F.J.R. Taylor 1976 (=*P. pacificum* Rampi)

1044 *Centrodinium pavillardii* F.J.R. Taylor 1976 (=*P. intermedium* (Pavillard 1916) de Toni 1936, *M. intermedia* Pavillard, non *C. intermedium* Pavillard 1930)

Tab. 1. – continued

1045 *Centrodinium porulosum* Kofoid 1911
1046 *Centrodinium punctatum* (Cleve 1900) F.J.R. Taylor 1976 (=*Steiniella punctata* Cleve, *M. punctata* (Cleve) Kofoid 1907, *P. punctatum* (Cleve) De Toni 1936, *Murrayella splendida* Rampi 1941, *P. splendidum* (Rampi) Rampi 1950)
1047 *Centrodinium pulchrum* Böhm 1933 (=*C. eminens* f. *pulchrum* (Böhm) Schiller 1933)
74 *Corythodinium* Loeblich Jr. *et* Loeblich III 1966 (=*Oxytoxum* Stein 1883 partim) (8 species)
1048 *Corythodinium belgicae* (Meunier 1910) F.J.R. Taylor 1976
1049 *Corythodinium carinatum* (Gaarder 1954) F.J.R. Taylor 1976
1050 *Corythodinium compressum* (Kofoid 1907) F.J.R. Taylor 1976
1051 *Corythodinium cristatum* (Kofoid 1907) F.J.R. Taylor 1976
1052 *Corythodinium curvicaudatum* (Kofoid 1907) F.J.R. Taylor 1976
1053 *Corythodinium diploconus* (Stein 1883) F.J.R. Taylor 1976
1054 *Corythodinium globosum* (Kofoid 1907) F.J.R. Taylor 1976 (=*Murrayella globosa* Kofoid, non *O. globosum* Schiller 1937)
1055 *Corythodinium recurvum* (Kofoid *et* Michener 1911) F.J.R. Taylor 1976
75 *Oxytoxum* Stein 1883 (42 species)
1056 *Oxytoxum adriaticum* Schiller 1937
1057 *Oxytoxum biconicum* (Kofoid 1907) Dodge *et* Saunders 1984 (=*Amphidoma biconica* Kofoid, *C. biconicum* (Kofoid) F.J.R. Taylor 1976, *Murrayella kofoidii* Gaarder 1954, *Pavillardinium kofoidii* (Gaarder) Sournia 1973)
1058 *Oxytoxum brunellii* Rampi 1939
1059 *Oxytoxum caudatum* Schiller 1937 (=*O. nanum* Halldal 1953, *O. rampii* Sournia 1973, *O. ligusticum* Rampi 1969)
1060 *Oxytoxum challengeroides* Kofoid 1907 (=?*O. minutum* Rampi 1941)
1061 *Oxytoxum constrictum* (Stein 1883) Bütschli 1885 (=*C. constrictum* (Stein) F.J.R. Taylor 1976)
1062 *Oxytoxum coronatum* Schiller 1937
1063 *Oxytoxum crassum* Schiller 1937 (=*O. globosum* Schiller 1937, non *C. globosum* (Kofoid 1907) F.J.R. Taylor 1976)
1064 *Oxytoxum cribosum* Stein 1883
1065 *Oxytoxum criophilum* Balech *in* Balech *et* El-Sayed 1965
1066 *Oxytoxum curvatum* (Kofoid 1907) Kofoid 1911 (=*Prorocentrum curvatum* Kofoid)
1067 *Oxytoxum depressum* Schiller 1937
1068 *Oxytoxum elegans* Pavillard 1916 (=*C. elegans* (Pavillard 1916) F.J.R. Taylor 1976)

Tab. 1. – continued

1069 *Oxytoxum elongatum* Wood 1963
1070 *Oxytoxum gladiolus* Stein 1883
1071 *Oxytoxum laticeps* Schiller 1937
1072 *Oxytoxum latum* Gaarder 1954
1073 *Oxytoxum longum* Schiller 1937
1074 *Oxytoxum michaelsarsii* Gaarder 1954
1075 *Oxytoxum milneri* Murray *et* Whitting 1899 (=*O. subulatum* Kofoid 1907)
1076 *Oxytoxum minutum* Rampi 1941 (=?*O. challengeroides* Kofoid 1907, resembles *O. lativelatum* F.J.R. Taylor 1976)
1077 *Oxytoxum mitra* Stein 1883
1078 *Oxytoxum mucronatum* Hope 1954
1079 *Oxytoxum obesum* Rampi 1969
1080 *Oxytoxum obliquum* Schiller 1937
1081 *Oxytoxum ovale* Schiller 1937 (=*O. mediterraneum* Schiller 1937, *O. punctulatum* Rampi 1951, *O. spinosum* Rampi 1941, *O. lativelatum* F.J.R. Taylor 1976)
1082 *Oxytoxum ovum* Gaarder 1954 (=?*C. globosum* (Kofoid 1907) F.J.R. Taylor 1976)
1083 *Oxytoxum pachyderme* Schiller 1937 *ex* F.J.R. Taylor 1976
1084 *Oxytoxum parvum* Schiller 1937 (=*O. tenuistriatum* Rampi 1943)
1085 *Oxytoxum pyramidale* Dodge *et* Saunders 1985
1086 *Oxytoxum radiosum* Rampi 1951
1087 *Oxytoxum reticulatum* (Stein 1883) Schütt 1896 (=*C. reticulatum* (Stein) Loeblich Jr. *et* Loeblich III 1966, *O. areolatum* Rampi 1941, *C. frenguellii* (Rampi 1941) F.J.R. Taylor 1976, *O. latum* Gaarder 1954, *C. latum* (Gaarder) F.J.R. Taylor 1976)
1088 *Oxytoxum robustum* Kofoid 1911
1089 *Oxytoxum sceptrum* (Stein 1883) Schröder 1906 (=*O. longiceps* Schiller 1937, *O. aceratum* Rampi 1951)
1090 *Oxytoxum scolopax* Stein 1883
1091 *Oxytoxum semicollatum* F.J.R. Taylor 1976
1092 *Oxytoxum sphaeroideum* Stein 1883 (=*Oxytoxum boehmii* Schiller 1937)
1093 *Oxytoxum strophalatum* Dodge *et* Saunders 1985
1094 *Oxytoxum tessellatum* (Stein 1883) Schütt 1895 (=*C. tessellatum* (Stein) Loeblich Jr. *et* Loeblich III 1966, *O. michaelsarsii* Gaarder 1954, *C. michaelsarsii* (Gaarder) F.J.R. Taylor 1976)

Tab. 1. – continued

1095 *Oxytoxum turbo* Kofoid 1907
1096 *Oxytoxum variabile* Schiller 1937 (=*O. gracile* Schiller 1937)
1097 *Oxytoxum viride* Schiller 1937
Pavillardinium* De-Toni 1936 (=***Amphidoma*** Stein 1883 partim, ***Centrodinium*** Kofoid 1907 partim, ***Murrayella*** Kofoid 1907)
**Pavillardinium ovale* (Pavillard 1930) De-Toni 1936 (=*Murrayella ovalis* Pavillard)
**Murrayella australica* Wood 1963
76 *Planodinium* Saunders *et* Dodge 1984
1098 *Planodinium striatum* Saunders *et* Dodge 1984
77 *Sabulodinium* Saunders *et* Dodge 1984
1099 *Sabulodinium inclinatum* (Balech 1956) Saunders *et* Dodge 1984 (=*Thecadinium inclinatum* Balech)
1100 *Sabulodinium undulatum* Saunders *et* Dodge 1984 (=*Phalacroma kofoidii* var. (colourless variety) Herdman 1924)
78 *Schuettiella* Balech 1988 (=***Gonyaulax*** Diesing 1866 partim, ***Oxytoxum*** Stein 1883 partim)
1101 *Schuettiella mitra* (Schütt 1895) Balech 1988 (=*Steinella mitra* Schütt, *Oxytoxum gigas* Kofoid 1907, *Gonyaulax mitra* (Schütt) Kofoid 1911)
79 *Thecadinium* Kofoid *et* Skogsberg 1928 (5 species)
**Thecadinium aureum* P.H. Campbell 1973
1102 *Thecadinium acanthium* Hoppenrath 2000 [Hoppenrath (2000b)]
1103 *Thecadinium dragescoi* Balech 1956
1104 *Thecadinium kofoidii* (Herdman 1923) J. Larsen 1985 (=*Amphidinium kofoidii* var. *petasatum* Herdman 1922, *T. petasatum* (Herdman) Balech, *Phalacroma kofoidii* Herdman 1924, *Amphidinium sulcatum* Kofoid sensu Herdman 1921, *T. kofoidii* Kofoid *et* Skogsberg *in* Schiller 1931, *T. petasatum* Kofoid *et* Skogsberg 1928)
1105 *Thecadinium neopetasatum* Saunders *et* Dodge 1984
1106 *Thecadinium ornatum* Hoppenrath 2000 [Hoppenrath (2000b)]

Insertae sedis

80 *Amphidiniella* Horiguchi 1995
1107 *Amphidiniella sedentaria* Horiguchi 1995 [Horiguchi (1995a)]

Peridiniaceae Ehrenberg 1830

81 *Bysmatrum* Faust *et* Steidinger 1998 [Faust and Steidinger (1998)]
1108 *Bysmatrum arenicola* Horiguchi *et* Pienaar 2000 (=*Scrippsiella arenicola* Horiguchi *et* Pienaar 1988, *B. arenicola* (Horiguchi *et* Pienaar) Faust *et* Steidinger 1998) [Faust and Steidinger (1998), Horiguchi and Pienaar (2000)]

Tab. 1. – continued

1109 *Bysmatrum granulosum* Ten-Hage, Quod, Turquet *et* Couté 2001 [Ten-Hage *et al.* (2001)]

1110 *Bysmatrum subsalsum* (Ostenfeld 1908) Faust *et* Steidinger 1998 (=*Peridinium subsalsum* Ostenfeld, *Scrippsiella subsalsa* (Ostenfeld) Steidinger *et* Balech 1977) [Faust and Steidinger (1998)]

82 ***Calciodinellum*** Deflandre 1947 [nomenclatural priority of fossil-encysted stage names does not have to be applied for dinoflagellate species (ICBN, Greuter *et al.* 2000)]

1111 *Calciodinellum albatrosianum* (Kamptner 1963) Janofske *et* Karwath 2000 [Janofske and Karwath (2000)]

1112 *Calciodinellum elongatum* (Hildebrand-Habel, Willems *et* Versteegh 1999) Meier, Janofske *et* Willems 2002) [Meier *et al.* (2002)]

1113 *Calciodinellum levantinum* Meier, Janofske *et* Willems 2002 [Meier *et al.* (2002)]

83 ***Ensiculifera*** Balech 1967 emend. Matsuoka, Kobayashi *et* Gaines 1990 (5 species)

1114 *Ensiculifera angulata* Balech 1988

1115 *Ensiculifera carinata* Matsuoka, Kobayashi *et* Gains 1990

1116 *Ensiculifera imariensis* Kobayashi *et* Matsuoka 1995 [Kobayashi and Matsuoka (1995)]

1117 *Ensiculifera loeblichii* Cox *et* Arnott 1971 (=*Pentapharsodinium trachodinium* Indelicato *et* Loeblich III 1986, *Peridinium loeblichii* (Cox *et* Arnott) Dale 1977)

84 ***Kryptoperidinium*** Lindemann 1924 (=***Glenodinium*** Ehrenberg 1836 partim)

1119 *Kryptoperidinium foliaceum* (Stein 1883) Lindemann 1924 (=*G. foliaceum* Stein,?*Peridinium cuneatum* van Goor 1925, *Phyllodinium scutelaris* Conrad 1926)

85 ***Pentapharsodinium*** Indelicato *et* Loeblich III 1986 (=***Peridinium*** Ehrenberg 1830 partim)

1120 *Pentapharsodinium tyrrhenicum* (Balech 1990) Montresor, Zingone *et* Marino 1993 (=*Peridinium tyrrhenicum* Balech) [Montresor *et al.* (1993)]

1121 *Pentapharsodinium dalei* Indelicato *et* Loeblich 1986 (=*Peridinium faeroense* sensu Dale 1977, *Scrippsiella faeroense* sensu Dodge 1982, *Peridinium dalei* (Indelicato *et* Loeblich III) Balech 1990, non *Peridinium faeroense* Paulsen 1905)

86 ***Peridinium*** Ehrenberg 1830 [nearly all freshwater species]

1122 *Peridinium gregarium* Lombard *et* Capon 1971 (=*Bysmatrum caponii* (Horiguchi *et* Pienaar 1988) Faust *et* Steidinger 1998, *Scrippsiella caponii* Horiguchi *et* Pienaar 1988, non *S. gregaria* (Lombard *et* Capon 1971) Loeblich III, Sherley *et* R.J. Schmidt 1979 =*S. hexapraecingula* Horiguchi *et* Chihara 1983) [Faust and Steidinger (1998)]

1123 *Peridinium quinquecorne* Abé 1927 (=*Protoperidinium quinquecorne* (Abé) Balech 1974,?*Heterocapsa quadridentata* Stein 1883)

87 ***Scrippsiella*** Balech 1959 *ex* Loeblich III 1965 (19 species)

1124 *Scrippsiella crystallina* J. Lewis 1991

1125 *Scrippsiella faeroensis* (Paulsen 1905) Balech *et* Soares 1967 (=*Calciodinellum faeroense* (Paulsen 1905) Havskum 1991, non *Scrippsiella faeroense* Dickensheets *et* Cox 1971=*S. trochoidea* (Stein 1883) Loeblich III 1976)

Tab. 1. – continued

1126 *Scrippsiella hangoei* (Schiller 1935) J. Larsen 1995 (=*Peridinium gracile* Lindemann 1924,?*P. novascotiense* Gran *et* Braarud 1935) [Larsen *et al.* (1995)]

1127 *Scrippsiella hexapraecingula* Horiguchi *et* Chihara 1983 (=*S. gregaria* (Lombard *et* Capon 1971) Loeblich III, Sherley *et* R.J. Schmidt 1979, non *Peridinium gregarium* Lombard *et* Capon)

**Scrippsiella iizukai* Kobayashi 1994 [described in a PhD, Kobayashi (1994)]

1128 *Scrippsiella infula* (Deflandre 1948) Montresor 2003 (=*Calcigonellum infula* Deflandre) [Montresor *et al.* (2003)]

1129 *Scrippsiella lachrymosa* J. Lewis 1991

1130 *Scrippsiella minima* Gao *et* Dodge 1991

1131 *Scrippsiella operosa* (Deflandre 1947) Montresor 2003 (=*Calciodinellum operosum* Deflandre) [Montresor *et al.* (2003)]

1132 *Scrippsiella patagonica* Akselman *et* Keupp 1990

1133 *Scrippsiella precaria* Montresor *et* Zingone 1988

1134 *Scrippsiella ramonii* Montresor 1995 [Montresor (1995)]

1135 *Scrippsiella regalis* (Gaarder 1954) Janofske 2000 (=*Discosphaera regalis* Gaarder) [Janofske (2000)]

1136 *Scrippsiella rotunda* J. Lewis 1991

1137 *Scrippsiella saladense* Balech 1963, "? saladensis"

1138 *Scrippsiella spinifera* Honsell *et* Cabrini 1991

1139 *Scrippsiella sweeneyae* Balech 1959 *ex* Loeblich III 1965 (=*S. sweeneyae* Wall *et* Dale 1968, *S. faeroense* sensu Dickensheets *et* Cox 1971)

1140 *Scrippsiella tinctoria* Indelicato *et* Loeblich III 1985

1141 *Scrippsiella trifida* J. Lewis 1991

**Scrippsiella triquetracapitata* Meier, Janofske *et* Willems 2002 [Meier *et al.* (2002)]

1142 *Scrippsiella trochoidea* (Stein 1883) Balech *ex* Loeblich III 1965 (=*Glenodinium trochoideum* Stein 1883, *G. acuminatum* Jørgensen 1899, *Peridinium trochoideum* (Stein 1883) Lemmermann 1910, *Peridinium faeroense* Paulsen 1905, *Scrippsiella faeroensis* (Paulsen 1905) Balech *et* Oliveira-Soares 1967, *Scrippsiella trochoidea* var. *aciculifera* Montresor 1999)

Protoperidiniaceae Balech 1988/*Protoperidiniaceae* J.P. Bujak *et* E.H. Davis 1998 (=*Kolkwitziellaceae* Lindemann 1928, *Diplopsaliaceae* Matsuoka 1988)

88 ***Boreadinium*** Dodge *et* Hermes 1981 (=***Diplopsalis*** Bergh 1881 partim)

1143 *Boreadinium breve* (Abé 1981) Sournia 1984 (=*Diplopsalis brevis* Abé)

1144 *Boreadinium pisiforme* Dodge *et* Hermes 1981

89 ***Diplopelta*** Stein 1883 *ex* Jørgensen 1912 (=***Dissodium*** Abé 1941 partim, ***Diplopsalis*** Bergh 1881 partim)

Tab. 1. – continued

1145 *Diplopelta excentrica* (Nie 1943) Balech (=*Diplopsalis excentrica* Nie, *Dissodium excentricum* (Nie) Loeblich III, *Peridiniopsis excentrica* (Nie) F.J.R. Taylor 1976, *Gotoius excentricus* (Nie) Sournia 1973)

1146 *Diplopelta pusilla* Balech *et* Akselman 1988

1147 *Diplopelta steinii* (Abé 1941) Balech 1988 (=*Diplopsalopsis steinii* Abé)

90 *Diplopsalis* Bergh 1881 (=***Glenodinium*** Ehrenberg 1836 partim, ***Dissodium*** Abé 1941 partim)

1148 *Diplopsalis lebourae* (Nie 1943) Balech 1967 (=*D. lenticula* var. *lebourae* Nie, non *Diplopsalis lebourae* Abé 1941, nec Abé 1981)

1149 *Diplopsalis lenticula* Bergh 1881 (=*Glenodinium lenticula* (Bergh) Schiller 1937, *Dissodium lenticulum* (Bergh) Loeblich III 1970, *Peridiniopsis lenticula* (Bergh) Starmach 1974)

**Diplopsalis minuta* Mangin 1912

**Diplopsalis sphaerica* Meunier 1910

91 *Diplopsalopsis* Meunier 1910 emend. Balech 1988 (=***Diplopsalis*** Bergh 1881 partim, ***Diplopelta*** Stein *ex* Jørgensen 1912 partim)

1150 *Diplopsalopsis bomba* (Stein 1883) Dodge *et* Toriumi 1993 (=*Diplopelta bomba* Stein *ex* Jørgensen 1912, *Diplopsalis asymmetrica* (Mangin 1911) Lindemann 1928,?*Diplopsalis asymmetrica* (Mangin) Abé 1941, *Peridiniopsis asymmetrica* Mangin 1911, *Dissodium asymmetricum* (Mangin) Loeblich III 1970, *Diplopelta symmetrica* Pavillard 1913) [Dodge and Toriumi (1993)]

1151 *Diplopsalopsis imitatio* (Balech 1979) Balech 1988 (=*Protoperidinium imitatio* Balech)

1152 *Diplopsalopsis globula* Abé 1941 (=*Diplopelta globulus* (Abé) Balech 1979, *Diplopsalopsis asymmetrica* (Mangin) var. *sphaerica* Mangin 1911, *Diplopsalopsis sphaerica* (Mangin) Balech 1962, *Dissodium globula* (Abé) Dodge *et* Hermes 1981)

1153 *Diplopsalopsis latipeltata* Balech *et* Borgese 1990

1154 *Diplopsalopsis orbicularis* (Paulsen 1907) Meunier 1910 (=*Peridinium orbiculare* Paulsen, *Diplopsalis orbicularis* (Paulsen) Paulsen 1930)

1155 *Diplopsalopsis ovata* (Abé 1941) Dodge *et* Toriumi 1993 (=*Diplopsalopsis orbicularis* (Paulsen 1907) var. *ovata* Abé 1941) [Dodge and Toriumi (1993)]

1156 *Diplopsalopsis pingii* (Nie 1943) Dodge *et* Toriumi 1993 (=*Diplopsalis pingii* Nie, *Peridiniopsis pingii* (Nie) F.J.R. Taylor 1976) [Dodge and Toriumi (1993)]

92 *Dissodium* Abé 1941 (=***Diplopsalis*** Bergh 1881 partim, ***Diplopelta*** Stein 1883 *ex* Jørgensen 1912 partim)

1157 *Dissodium parvum* Abé 1941 (=*Diplopelta parva* (Abé) Matsuoka 1988, *Diplopsalis parvum* (Abé) Abé 1981)

93 *Gotoius* Abé 1981 *ex* Matsuoka 1988 (=***Diplopsalis*** Bergh 1881 partim, ***Dissodium*** Abé 1941 partim)

1158 *Gotoius abei* Matsuoka 1988

Tab. 1. – continued

1159 *Gotoius excentricus* (Nie 1943) Sournia 1984 (=*Diplopsalis excentrica* Nie 1943, *Dissodium excentricum* (Nie) Loeblich III 1970, *Peridiniopsis excentrica* (Nie) F.J.R. Taylor 1976)

1160 *Gotoius mutsuensis* Abé 1981 *ex* Matsuoka 1988

1161 *Gotoius ostenfeldii* (Steemann Nielsen 1931) Dodge *et* Toriumi 1993 (=*Diplopsalis ostenfeldii* Steemann Nielsen) [Dodge and Toriumi (1993)]

94 ***Lebouraia*** Abé 1941 *ex* Sournia 1986 (=***Diplopsalis*** Bergh 1881 partim, ***Diplopelta*** Stein *ex* Jørgensen 1912 partim)

1162 *Lebouraia minuta* Abé 1941 (=*Diplopsalis minuta* (Abé) Abé 1981)

1163 *Lebouraia pusilla* (Balech *et* Akselman 1988) Dodge *et* Toriumi 1993 (=*Diplopelta pusilla* Balech *et* Akselman) [Dodge and Toriumi (1993)]

95 ***Oblea*** Balech 1964 (=***Peridiniopsis*** Lemmermann 1904 partim, ***Diplopsalis*** Bergh 1881 partim)

1164 *Oblea baculifera* Balech 1964 *ex* Loeblich Jr. *et* Loeblich III 1966

1165 *Oblea rotunda* (Lebour 1922) Balech 1964 *ex* Sournia 1973 (=*Peridiniopsis rotunda* Lebour, *Glenodinium rotundum* (Lebour) Schiller 1937, *Diplopsalis rotunda* (Lebour) Wood 1954, *Diplopsalis rotundata* Steidinger *et* Williams 1970)

1166 *Oblea torta* (Abé 1941) Balech 1964 *ex* Sournia 1973 (=*Diplopsalis torta* Abé, *Diplopsalis hainanensis* Nie 1943, *Peridiniopsis hainanensis* (Nie) F.J.R. Taylor 1976)

96 ***Preperidinium*** Mangin 1913 (=***Diplopeltopsis*** Pavillard 1913, ***Zygabikodinium*** Loeblich Jr. *et* Loeblich III 1970)

1167 *Preperidinium granulosum* (Balech 1958) Elbrächter 1993 (=*Diplopeltopsis granulosa* Balech, *Zygabikodinium granulatum* (Balech) Loeblich III 1970) [Elbrächter (1993)]

1168 *Preperidinium meunieri* (Pavillard 1907) Elbrächter 1993 (=*Diplopsalis lenticula* Bergh f. *minor* Paulsen 1907, *Zygabikodinium lenticulatum* Loeblich Jr. *et* Loeblich III 1970, *Peridinium lenticulum* Mangin 1911, *Peridinium paulsenii* Mangin 1911, *Glenodinium lenticula* f. *minor* (Paulsen 1907) Pavillard 1913, *Diplopeltopsis minor* (Paulsen 1907) Pavillard 1913, *Peridiniopsis minor* (Paulsen) Starmach 1974) [Elbrächter (1993)]

1169 *Preperidinium perlatum* (Balech 1971) Elbrächter 1993 (=*Diplopeltopsis perlata* Balech 1971, *Zygabikodinium perlatum* (Balech) Elbrächter 1975) [Elbrächter (1993)]

1170 *Preperidinium pseudo-oblea* (Elbrächter 1975) Elbrächter 1993 (=*Zygabikodinium pseudo-oblea* Elbrächter) [Elbrächter (1993)]

97 ***Protoperidinium*** Bergh 1881 emend. Balech 1974 (=***Peridinium*** Ehrenberg 1830 partim, ***Minuscula*** Lebour 1925) (264 species)

1171 *Protoperidinium abei* (Paulsen 1930) Balech 1974 (=*P. biconicum* Abé 1927, non *P. biconicum* P. Dangeard 1927)

1172 *Protoperidinium acanthophorum* (Balech 1962) Balech 1974 (=*P. rhomboidalis* Abé 1981, *P. cerassiformis* Abé 1981)

1173 *Protoperidinium achromaticum* (Levander 1902) Balech 1974 (=*P. achromaticum* Levander, related to *Protoperidinium finitimum* Balech 1976)

1174 *Protoperidinium acutipes* (P. Dangeard 1927) Balech 1974 (=*P. quadratum* Matzenauer 1933, *P. divergens* f. *acutipes* (P. Dangeard) Schiller 1937)

1175 *Protoperidinium acutum* (Fauré-Fremiet 1908) Balech 1974 (=*P. pellucidum* var. *acutum* Fauré-Fremiet)

Tab. 1. – continued

1176 *Protoperidinium adeliense* (Balech 1959) Balech 1974
1177 *Protoperidinium adense* (Matzenauer 1933) Balech 1974
1178 *Protoperidinium adulterum* (Balech 1971) Balech 1974
1179 *Protoperidinium aequatoriale* (Balech 1971) Balech 1974
1180 *Protoperidinium affine* (Balech 1958) Balech 1974
1181 *Protoperidinium aliferum* (Gaarder *in* Parke *et* Dixon 1968) Balech 1974 (=*P. matzenaueri* Gaarder 1954, non *P. matzenaueri* Böhm 1936)
1182 *Protoperidinium americanum* (Gran *et* Braarud 1935) Balech 1974
1183 *Protoperidinium amplum* (Matzenauer 1933) Balech 1974
1184 *Protoperidinium ampulla* (Balech 1971) Balech 1974 (=*P. granii* var. *mite* f. *spirale* Gaarder 1954)
1185 *Protoperidinium anceps* (Meunier 1910) Balech 1974
1186 *Protoperidinium anguipes* (Balech 1967) Balech 1974
1187 *Protoperidinium angustum* (P. Dangeard 1932) Balech 1974 (=?*Protoperidinium wiesneri* (Schiller 1931) Balech 1974)
1188 *Protoperidinium anomaloplaxum* (Balech 1964) Balech 1974
1189 *Protoperidinium antarcticum* (Schimper *in* Karsten 1905) Balech 1974 (non *P. depressum* var. *parallelum* (Broch) Balech 1994) [Balech (1994a)]
1190 *Protoperidinium anthonyi* (Fauré-Fremiet 1908) Balech 1974
1191 *Protoperidinium applanatum* (Mangin 1914) Balech 1974 (=*P. obovatum* Wood 1954)
1192 *Protoperidinium archiovatum* (Balech 1958) Balech 1974
1193 *Protoperidinium arcticum* (Grøntved *et* Seidenfaden 1938) Okolodkov 1997 (=*P. ovatum* f. *arctica* Grøntved *et* Seidenfaden) [Okolodkov (1997)]
1194 *Protoperidinium areolatum* (Peters 1928) Balech 1974
1195 *Protoperidinium argentiniense* Balech 1979
1196 *Protoperidinium asperum* (Wailes 1928) Balech 1974
1197 *Protoperidinium aspidiotum* (Balech 1964) Balech 1974
1198 *Protoperidinium asymmetricum* Balech 1974 (=*P.* (*Sphaeridinium*) *asymmetricum* (Abé 1927) Abé 1981, non *P. asymmetricum* Karsten 1907)
1199 *Protoperidinium avellana* (Meunier 1919) Balech 1974 (=*Properidinium avellana* Meunier)
1200 *Protoperidinium balechii* (Akselman 1972) Balech 1988
1201 *Protoperidinium belizeanum* Faust 2003 (non *Peridinium belizense* Carty *et* Wujek 2003, published as »belizensis« ICBN Art. 23.5 and 32.5) [Faust (2003), Carty and Wujek (2003)] (the epithet »belizianum« is orthographically correct, ICBN Art. 60.1)
1202 *Protoperidinium bellulum* (Balech 1971) Balech 1974
1203 *Protoperidinium biconicum* (P. Dangeard 1927) Balech 1974 (non *P. biconicum* Abé 1936)

Tab. 1. – continued

1204 *Protoperidinium bidentatum* (Abé 1981) Balech 1994 (=*P. bidentatum* Abé 1981) [Balech (1994a)]
1205 *Protoperidinium bipatens* Balech 1973
1206 *Protoperidinium bipes* (Paulsen 1904) Balech 1974 (=*Minuscula bipes* (Paulsen) Lebour 1925, *Glenodinium bipes* Paulsen 1904, *Peridinium minusculum* Pavillard 1905, non *Peridinium bipes* Stein 1883)
1207 *Protoperidinium bispinum* (Schiller 1937) Balech 1974 (=?*P. bimucronatum* (Schiller 1937) Balech 1974, non *Protoperidinium sourniai* (F.J.R. Taylor 1976) Balech 1994) [Balech (1994a)]
1208 *Protoperidinium bourrellyi* Balech 1999 [Balech (1999)]
1209 *Protoperidinium braarudii* (Schiller 1937) Balech 1974
1210 *Protoperidinium brevipes* (Paulsen 1908) Balech 1974 (=*P. brevipes* Paulsen, *P. varicans* Paulsen 1911, *P. incurvum* Lindemann 1924)
1211 *Protoperidinium brochii* (Kofoid *et* Swezy 1921) Balech 1974 (=*P. adriaticum* Broch 1920, non *P. adriaticum* Schmarda 1846)
1212 *Protoperidinium bulbosum* (Gaarder 1954) Balech 1974
1213 *Protoperidinium bulla* (Meunier 1910) Balech 1974
1214 *Protoperidinium capdevillei* (Balech 1959) Balech 1974 (=?*P. pacificum* Kofoid *et* Michener 1911)
1215 *Protoperidinium capurroi* (Balech 1959) Balech 1974 (=?*P. brachypus* Abé 1981, non *P. brachypus* Schiller 1937)
1216 *Protoperidinium carinaeferum* (Gail 1950) Balech 1994 (=*P. arinaeferum* Gail) [Balech (1994a)]
1217 *Protoperidinium carum* (Abé 1981) Balech 1994 (=*P. carus* Abé) [Balech (1994a)]
1218 *Protoperidinium cassum* (Balech 1971) Balech 1974 (=*Protoperidinium cassum cassum* Balech 1988)
Protoperidinium cassum var. *decens* Balech 1988 (=*Protoperidinium decens* (Balech 1971) Balech 1974)
1219 *Protoperidinium castaneiforme* (Mangin 1922) Balech 1974
1220 *Protoperidinium cavispinum* (Mangin 1922) Balech 1974
1221 *Protoperidinium cepa* (Balech 1971) Balech 1974
1222 *Protoperidinium cerasus* (Paulsen 1907) Balech 1973
1223 *Protoperidinium charcotii* (Balech 1958) Balech 1974
1224 *Protoperidinium claudicans* (Paulsen 1907) Balech 1974
1225 *Protoperidinium claudum* Balech 1994 (=*P. asymmetricum* Karsten sensu Böhm 1936, non Karsten 1907) [Balech (1994a)]
1226 *Protoperidinium colombonense* (Matzenauer 1933) Balech 1974
1227 *Protoperidinium compressum* (Abé 1927) Balech 1974 (=*Congruentidium compressum* Abé 1927, *P. compressum* Abé 1981, non *P. stellatum* Wall *et* Dale 1968)
1228 *Protoperidinium concavum* (Mangin 1926) Balech 1974 (=?*Protoperidinium granii* (Ostenfeld 1906) Balech 1974, *P. petersii* Balech 1958)

Tab. 1. – continued

1229 *Protoperidinium conicoides* (Paulsen 1905) Balech 1973
1230 *Protoperidinium conicum* (Gran 1900) Balech 1974 (=*P. divergens* var. *conica* Gran)
1231 *Protoperidinium consimile* (Abé 1981) Balech 1994 (=*P. consimilis* Abé) [Balech (1994a)]
1232 *Protoperidinium corniculum* (Kofoid *et* Michener 1911) F.J.R. Taylor *et* Balech *in* Balech 1979
1233 *Protoperidinium cornutum* (Karsten 1907) Balech 1974
1234 *Protoperidinium crassipes* (Kofoid 1907) Balech 1974 [see Balech (1988:110) for synonymy with *Protoperidinium curtipes* (Jørgensen 1912) Balech 1974]
1235 *Protoperidinium crassipyrum* (Balech 1961) Balech 1974 (=*P. crassum* Balech (1959) Balech 1974, non *P. crassum* P. Dangeard 1927)
1236 *Protoperidinium cristatum* Balech 1979
1237 *Protoperidinium cruciferum* (Balech 1971) Balech 1973 (=?*P. parvum* Abé 1981)
1238 *Protoperidinium curtipes* (Jørgensen 1912) Balech 1974 (=*P. curtipes* Jørgensen 1912, *P. crassipes* Paulsen 1907 partim, non *P. crassipes* Paulsen 1930, nec Schiller 1937)
1239 *Protoperidinium curtum* (Balech 1958) Balech 1973
1240 *Protoperidinium curvipes* (Ostenfeld 1906) Balech 1974
1241 *Protoperidinium cuspidatum* Balech 1979
1242 *Protoperidinium dakariense* (P. Dangeard 1927) Balech 1974 (=*P. gibbosum* Matzenauer (1933) Balech 1974, *P. parvispinum* Gaarder 1954)
1243 *Protoperidinium decipiens* (Jørgensen 1899) Parke *et* Dodge 1976
1244 *Protoperidinium decollatum* (Balech 1971) Balech 1974
1245 *Protoperidinium defectum* (Balech *in* Balech *et* El-Sayed 1965) Balech 1974
1246 *Protoperidinium deficiens* (Meunier 1919) Balech 1974
1247 *Protoperidinium denticulatum* (Gran *et* Braarud 1935) Balech 1974 (=*P. clavus* Abé 1936)
1248 *Protoperidinium depressum* (Bailey 1850) Balech 1974 (=*P. parallelum* Broch 1906, non *P. antarcticum* Schimper, *P. marinum* Lindemann 1925, *P. claudicanoides* Graham 1942), *Protoperidinium depressum* subsp. *convexius* (Graham 1941) Balech 1994 [Balech (1994a)]
1249 *Protoperidinium diabolus* (Cleve 1900) Balech 1974 (=*P. longipes* Karsten 1907)
1250 *Protoperidinium discoides* (Wailes 1928) Balech 1974
1251 *Protoperidinium divaricatum* (Meunier 1919) Parke *et* Dodge 1976 (=*P. gainii* (P. Dangeard 1927) Balech 1974, *P. divaricatum* (Meunier) Balech 1988)
1252 *Protoperidinium divergens* (Ehrenberg 1841) Balech 1974

Tab. 1. – continued

**Protoperidinium dodgei* Okolodkov 1997 [Okolodkov (1997), not included in Okolodkov and Dodge (1997)]
1253 *Protoperidinium dolichoporum* Borgese 1987
1254 *Protoperidinium elegans* (Cleve 1900) Balech 1974 (=*P. annulatum* Kofoid *et* Michener 1911,?*P. elegans* Matzenauer 1933)
1255 *Protoperidinium elegantissimum* (Balech 1958) Balech 1974
1256 *Protoperidinium ellipticum* Halim 1969
1257 *Protoperidinium elongatum* (Meunier 1910) Balech 1974
1258 *Protoperidinium exageratum* Balech 1979 (=*P. globulus* var. *quarnerense* f. *spirale* Gaarder 1954)
1259 *Protoperidinium excentricum* (Paulsen 1907) Balech 1974 (=*P. excentricum* Paulsen, *Peridinium perrieri* Fauré-Frémient 1909)
1260 *Protoperidinium exiguipes* (Mangin 1930 *ex* Halim 1968) Dodge 1985
1261 *Protoperidinium exiguum* (Cleve 1900) Balech 1974
1262 *Protoperidinium exile* Balech 1994 (=*P. gracile* Meunier 1910) [Balech (1994a)]
**Protoperidinium falk-petersenii* Okolodkov 1999 [Okolodkov (1999)]
1263 *Protoperidinium fastum* Balech 1979
1264 *Protoperidinium faurei* Balech 1994 (=*P. ovatum* Pouchet var.? Fauré-Fremiet 1908) [Balech (1994a)]
1265 *Protoperidinium fimbriatum* (Meunier 1919) Balech 1974
1266 *Protoperidinium finitimum* Balech 1976 [related to *P. achromaticum* (Levander 1902) Balech 1974]
1267 *Protoperidinium formosum* (Pavillard 1909) Balech 1974 (=*P. diabolus* var. *formosum* (Pavillard) F.J.R. Taylor 1976)
1268 *Protoperidinium furcatum* (Abé 1981) Balech 1994 (=*P. furcatum* Abé) [Balech (1994a)]
1269 *Protoperidinium gaarderae* (Balech 1967) Balech 1974
1270 *Protoperidinium gibberum* (Abé 1981) Balech 1994 (=*P. gibberum* Abé, non *P. okamurai* Abé 1927, non *P. okamurai* Yoneda *et* Marukawa *in* Marukawa 1921) [Balech (1994a)]
1271 *Protoperidinium globiferum* (Abé 1981) Balech 1994 (=*P. globifera* Abé) [Balech (1994a)]
1272 *Protoperidinium globulus* (Stein 1883) Balech 1974 (=*P. ovatum* (Pouchet) Schütt 1895)
1273 *Protoperidinium glyptopterum* Balech 1973
1274 *Protoperidinium grahamii* (Sournia 1973) Balech 1994 (=*P. grahamii* Sournia, *P. truncatum* Graham 1942, non *P. truncatum* Zacharias 1903) [Balech (1994a)]
1275 *Protoperidinium grande* (Kofoid 1907) Balech 1974 (=*P. elegans* Matzenauer 1933, non *P. grande* P. Dangeard 1927)
1276 *Protoperidinium granii* (Ostenfeld 1906) Balech 1974 (non *Peridinium gracile* Gran *et* Braarud 1935) [Balech (1994a)]
1277 *Protoperidinium grenlandicum* (Woloszyńska 1916) Balech 1974

Tab. 1. – continued

1278 *Protoperidinium hamatum* Balech 1979
1279 *Protoperidinium helix* (Balech 1962) Balech 1974
1280 *Protoperidinium hemisphaericum* (Abé 1936) Balech 1988
1281 *Protoperidinium heteracantlium* (P. Dangeard 1927) Balech 1974 (non *Protoperidinium norpacense* Balech 1974)
1282 *Protoperidinium heteroconicum* (Matzenauer 1933) Balech 1974
1283 *Protoperidinium heterospinum* (Gaarder 1954) Balech 1974
1284 *Protoperidinium hidemitii* (Paulsen 1949) Balech 1994 (=*P. rotundatum* Abé 1936, non *P. rotundatum* Karsten 1907) [Balech (1994a)]
1285 *Protoperidinium hirobis* (Abé 1927) Balech 1974
1286 *Protoperidinium huberi* (Schiller 1929) Balech 1974
1287 *Protoperidinium humile* (Schiller 1937) Balech 1974 (=*P. perbreve* Balech *et* Soares 1967)
1288 *Protoperidinium hyalinum* (Meunier 1910) Balech 1974
1289 *Protoperidinium illepidum* Balech 1994 (=*P. pellucidum* var. *crassum* Fauré-Fremiet 1908) [Balech (1994a)]
1290 *Protoperidinium incertum* (Balech 1958) Balech 1973
1291 *Protoperidinium inclinatum* (Balech 1964) Balech 1974 (=*P. sphaericum* Okamura 1912)
1292 *Protoperidinium incognitum* (Balech 1959) Balech 1974
1293 *Protoperidinium inflatiforme* (Böhm 1936) Balech 1974
1294 *Protoperidinium inflatum* (Okamura 1912) Balech 1974 (=*P. inflatum* Okamura, *P. brochii* (Okamura) f. *inflatum* Schiller 1937, *P. crassum* P. Dangeard 1927)
1295 *Protoperidinium islandicum* (Paulsen 1904) Balech 1973
1296 *Protoperidinium isthmus* (Abé 1981) Balech 1994
1297 *Protoperidinium joergensenii* (Balech 1971) Balech 1974 (=*P. pedunculatum* Jørgensen 1905, non *P. pedunculatum* Schütt 1895)
1298 *Protoperidinium joubinii* (P. Dangeard 1927) Balech 1974
**Protoperidinium knipowitschii* (Usachev 1927) Balech 1974
1299 *Protoperidinium laciniosum* Balech 1994 (=*P. petersii* Abé 1981, non *P. petersii* Balech 1958) [Balech (1994a)]
1300 *Protoperidinium laticeps* (Grøntved *et* Seidenfaden 1938) Balech 1974 (=*P. laticeps* Grøntved *et* Seidenfaden) [=*?P. consimile* (Abé 1981) Balech 1994]
1301 *Protoperidinium latidorsale* (P. Dangeard 1927) Balech 1974 (=*P. oblongum* var. *latidorsale* P. Dangeard)
1302 *Protoperidinium latipyrum* (Balech 1959) Balech 1974

Tab. 1. – continued

1303 *Protoperidinium latispinum* (Mangin 1926) Balech 1974 (=*P. africanoides* (P. Dangeard 1927) Balech 1974, *P. angusticollum* Abé 1981,?*P. sylvanae* P. Dangeard 1927)

1304 *Protoperidinium latissimum* (Kofoid 1907) Balech 1974 (=*P. pentagonoides* Balech 1949, *P. pentagonum* var. *latissimum* (Kofoid) Schiller 1937, *Protoperidinium exiquipes* (Mangin 1930) Dodge 1985)

1305 *Protoperidinium latistriatum* (Balech 1958) Balech 1974

1306 *Protoperidinium leonis* (Pavillard 1916) Balech 1974 (=*P. conicum* Meunier 1919)

1307 *Protoperidinium ligusticum* (Rampi 1951) Balech 1974

1308 *Protoperidinium lipopodium* (Balech 1964) Balech 1974 (=*P. subcurvipes* Balech 1959, non *P. subcurvipes* Lebour 1923)

1309 *Protoperidinium longipes* Balech 1974 (=*Protoperidinium longipes* (Karsten 1907) Balech 1974, *P. diabolus* var. *longipes* (Karsten) F.J.R. Taylor 1976)

1310 *Protoperidinium longispinum* (Kofoid 1907) Balech 1974 (=*P. michaelis* Ehrenberg 1840 partim, non *P. longispinum* Mangin 1930)

1311 *Protoperidinium macrapicatum* (Balech 1971) Balech 1973 (=?*P. gracile* Gran *et* Braarud 1935)

1312 *Protoperidinium magnum* (Schiller 1929) Balech 1974 (=?*P. crassipes* Kofoid 1907)

1313 *Protoperidinium majus* (P. Dangeard 1927) Balech 1974 (=*P. ovatum* var. *majus* P. Dangeard)

1314 *Protoperidinium manginii* (Balech 1971) Balech 1974 (=*P. pyriforme* Peters 1928)

1315 *Protoperidinium maranense* Tolomio 1981

1316 *Protoperidinium marielebourae* (Paulsen 1931) Balech 1974 (=*P. obtusum* (Karsten 1906) Lebour 1925, *non P. obtusum* (Karsten) Fauré-Fremiet 1980)

1317 *Protoperidinium marukawai* (Abé 1936) Balech 1974

1318 *Protoperidinium mastophorum* (Balech 1971) Balech 1974 (=*P. granii* Matzenauer 1933, non *P. granii* Ostenfeld 1906)

1319 *Protoperidinium mediocre* (Balech 1958) Balech 1974

1320 *Protoperidinium mediterraneum* (Kofoid 1909) Balech 1974 (=*P. longicollum* Pavillard 1916, *P. steinii* subsp. *mediterraneum* Kofoid)

1321 *Protoperidinium melo* (Balech 1971) Balech 1974

1322 *Protoperidinium mendiolae* Balech 1978

1323 *Protoperidinium metananum* (Balech *in* Balech *et* El-Sayed 1965) Balech 1974

**Protoperidinium minus* (Mangin 1926) Balech 1974

**Protoperidinium minutissimum* (Mangin 1926) Balech 1974

1324 *Protoperidinium minutum* (Kofoid 1907) Loeblich III 1970 [see *P. monospinum* (Paulsen 1907) Zonneveld *et* Dale 1994] [Zonneveld and Dale (1994)]

Tab. 1. – continued

1325 *Protoperidinium mite* (Pavillard 1916) Balech 1974 (=*P. granii* Ostenfeld f. *mite* (Pavillard) Schiller 1937)
1326 *Protoperidinium monacanthum* (Broch 1910) Balech 1973 (=*P. complanatum* Meunier 1910)
1327 *Protoperidinium monospinum* (Paulsen 1907) Zonneveld *et* Dale 1994 (=*P. constrictum* (Abé 1936) Balech 1974, *P. constricta* Abé) [the synonymy with *Protoperidinium minutum* is debatable] [Zonneveld and Dale (1994)]
1328 *Protoperidinium monovelum* (Abé 1936) Balech 1974
1329 *Protoperidinium multipunctatum* (Fauré-Fremiet 1908) Balech 1994 (=*P. multipunctatum* Fauré-Fremiet) [Balech (1994a)]
1330 *Protoperidinium munobis* (Abé 1927) Balech 1974
1331 *Protoperidinium murrayi* (Kofoid 1907) Hernández-Becerril 1991 (=*P. murrayi* Kofoid 1907, *P. murrayi* var. *occidentalis* Pavillard 1930, *P. murrayi* var. *orientalis* Matzenauer) [synonym of *P. oceanicum* (Vanhöffen 1897) Balech 1974 sec Balech (1988)]
1332 *Protoperidinium mutsuense* (Abé 1936) Balech 1974 (=*P. mutsuensis* Abé)
1333 *Protoperidinium nanum* (Balech 1962) Balech 1974
1334 *Protoperidinium norpacense* (Balech 1962) Balech 1974 (=*P. heteracanthum* P. Dangeard *sec* Matzenauer 1933, non *P. heteracanthum* P. Dangeard 1927)
1335 *Protoperidinium novascotiense* (Gran *et* Braarud 1935) Balech 1974 (=?*Scrippsiella hangoei* (Schiller 1935) J. Larsen 1995) [Larsen *et al.* (1995)]
1336 *Protoperidinium nudum* (Meunier 1910) Balech 1974
**Protoperidinium nux* (Schiller 1937) Balech 1974 (=*P. levanderi* Abé 1927, *P. aequilimbus* Abé 1981)
1337 *Protoperidinium obesum* (Matzenauer 1933) Balech 1974
1338 *Protoperidinium oblongum* (Aurivillius 1898) Parke *et* Dodge 1976 (=*P. divergens* var. *oblongum* Aurivillius)
1339 *Protoperidinium obtusipes* (Mangin 1930) Balech 1974
1340 *Protoperidinium obtusum* (Karsten 1906) Parke *et* Dodge 1976 (=*Protoperidinium obtusum* (Karsten) Balech 1988, *P. divergens* Ehrenberg var. *obtusum* Karsten, *P. okamurai* Marukawa 1921, non *P. okamurai* Abé 1927, *P. obtusum* Schiller 1937, non *P. obtusum* Fauré-Fremiet 1908)
1341 *Protoperidinium oceanicum* (Vanhöffen 1897) Balech 1974 (=*P. oceanicum* Vanhöffen) [also *Peridinium murrayi* Kofoid 1907 sec Balech (1988)]
1342 *Protoperidinium okamurai* Yoneda *et* Marukawa *in* Marukawa 1921 (non *Protoperidinium gibberum* (Abé 1981) Balech 1994) [Balech (1994a)]
1343 *Protoperidinium orientale* (Matzenauer 1933) Balech 1974
1344 *Protoperidinium ovatoides* (Meunier 1910) Balech 1974

Tab. 1. – continued

1345 *Protoperidinium ovatum* Pouchet 1883 (=*P. lenticulatum* Fauré-Fremiet 1908), *Protoperidinium ovatum* ssp. *asymmetricum* (P. Dangeard 1927) Balech 1988)

1346 *Protoperidinium oviforme* (P. Dangeard 1927) Balech 1974

1347 *Protoperidinium ovum* (Schiller 1911) Balech 1974 (=*Protoperidinium nipponicum* (Abé 1927) Balech 1974, *P. ovum* Schiller 1911,?*P. ellipsoides* P. Dangeard 1927, *P. ellipsoideum* P. Dangeard 1927, non *P. ovum* Mangin 1912)

1348 *Protoperidinium pacificum* (Kofoid *et* Michener 1911) F.J.R. Taylor *et* Balech *ex* Balech 1988 (=*P. capdevillei* Balech 1959) Balech 1974)

1349 *Protoperidinium pallidum* (Ostenfeld 1899) Balech 1973

1350 *Protoperidinium paradoxum* (F.J.R. Taylor 1976) Balech 1994 (=*P. paradoxum* F.J.R. Taylor) [Balech (1994a)]

1351 *Protoperidinium parapyriforme* (Hermosilla 1968) Balech 1974

1352 *Protoperidinium parcum* (Balech 1971) Balech 1974

1353 *Protoperidinium parthenopes* Zingone *et* Montresor 1988

1354 *Protoperidinium parvicollum* (Balech 1958) Balech 1973

1355 *Protoperidinium parvispinum* (Gaarder 1954) Balech 1974

1356 *Protoperidinium parviventer* Balech 1978 (=?*P. gracile* Gran *et* Braarud 1935)

1357 *Protoperidinium paulsenii* (Pavillard 1909) Balech 1974 (non *P. paulsenii* Mangin 1911, non *P. paulsenii* Abé 1981=*P. subinerme* Paulsen 1931)

1358 *Protoperidinium pedunculatum* (Schütt 1895) Balech 1974

1359 *Protoperidinium pellucidum* Bergh 1881 *ex* Loeblich Jr. *et* Loeblich III 1966 (=*P. pellucidum* (Bergh) Schütt 1895, non Pouchet 1883, nec Vanhöffen 1897), *P. pellucidum* ssp. *asteriferum* Balech 1994 (=*P. pellucidum* ssp. *stellatum* Balech 1978, non *Peridinium stellatum* Wall 1968) [Balech (1994a)]

1360 *Protoperidinium penitum* (Balech 1971) Balech 1974 (=*P. ovatum* Peters 1928)

1361 *Protoperidinium pentagonum* (Gran 1902) Balech 1974 (=*P. divergens* var. *sinuosum* Lemmermann 1899, *P. sinuosum* Lemmermann 1905, *P. parapentagonum* Wang 1936, *P. expansum* Abé 1981, *non P. pentagonum* P. Dangeard 1926)

1362 *Protoperidinium perplexum* (Balech 1971) Balech 1974

1363 *Protoperidinium perradiatum* Balech 1978

1364 *Protoperidinium persicum* Schiller 1937 (=*P. schilleri* Böhm 1931, *P. matzenaueri* Böhm 1936, *P. margalefii* E.S. Silva 1965)

1365 *Protoperidinium peruvianum* (Balech 1961) Balech 1974

1366 *Protoperidinium pietschmannii* (Böhm 1931) Balech 1974

1367 *Protoperidinium planiceps* (Abé 1981) Balech 1988 (=*P. thorianum* var. *planiceps* Abé)

1368 *Protoperidinium platifrons* Balech 1999 [Balech (1999)]

Tab. 1. – continued

1369 *Protoperidinium porosum* Balech 1978
1370 *Protoperidinium pouchetii* (Kofoid *et* Michener 1911) F.J.R. Taylor *et* Balech *ex* Balech 1988 (=*P. brintonii* Balech 1962)
1371 *Protoperidinium pseudoantarcticum* (Balech 1958) Balech 1974
1372 *Protoperidinium pseudogranii* (Peters 1930) Balech 1994 (=*P. pseudogranii* Peters) [Balech (1994a)]
1373 *Protoperidinium pseudopallidum* (Peters 1930) Balech 1994 (=*P. pseudopallidum* Peters) [Balech (1994a)]
1374 *Protoperidinium punctulatum* (Paulsen 1908) Balech 1974 (non *Peridinium punctulatum* Paulsen 1931=*P. multistriatum* Kofoid 1907)
1375 *Protoperidinium pyriforme* (Paulsen 1907) Balech 1974 (=*P. steinii* var. *pyriformis* Paulsen 1905, *P. pyriforme* spp. *pyriforme* (Paulsen) Balech 1988) *Protoperidinium pyriforme* ssp. *breve* (Paulsen 1907) Balech 1988 (=*P. breve* (Paulsen 1907) Balech)
1376 *Protoperidinium pyrum* (Balech 1959) Balech 1974
1377 *Protoperidinium quadratum* (Matzenauer 1933) Balech 1974
1378 *Protoperidinium quarnerense* (Schröder 1900) Balech 1974 (=*P. globulus* var. *quarnerense* Schröder)
1379 *Protoperidinium radius* (Balech 1971) Balech 1976 (=*Peridinium concavum* subsp. *radius* Balech)
1380 *Protoperidinium rampii* (Balech 1959) Balech 1974
1381 *Protoperidinium raphanus* (Balech 1958) Balech 1974
1382 *Protoperidinium rectius* (Graham 1942) Balech 1994 (=*P. depressum* var. *rectius* Graham) [Balech (1994a)]
1383 *Protoperidinium rectum* (Kofoid 1907) Balech 1974
1384 *Protoperidinium retiferum* (Matzenauer 1933) Balech 1978
1385 *Protoperidinium rhombiforme* (Abé 1981) Balech 1994 (=*P. rhombiformis* Abé) [Balech (1994a)]
1386 *Protoperidinium robustum* (Meunier 1910) Hernández-Becerril 1991
1387 *Protoperidinium rosaceum* (Balech 1958) Balech 1974
1388 *Protoperidinium roscoffiense* (Balech 1962) Balech 1974
1389 *Protoperidinium roseum* (Paulsen 1904) Balech 1974
1390 *Protoperidinium saltans* (Meunier 1910) Balech 1973 (=*P. valgus* Abé 1981)
1391 *Protoperidinium schilleri* (Paulsen 1930) Balech 1974 (=*P. pallidum* var. *schilleri* (Paulsen) Schiller 1937, non *P. schilleri* Böhm 1931)
**Protoperidinium schuettii* Halim 1969
1392 *Protoperidinium simulum* (Paulsen 1931) Balech 1931
1393 *Protoperidinium sinaicum* (Matzenauer 1933) Balech 1974

Tab. 1. – continued

1394 *Protoperidinium solidicorne* (Mangin 1922) Balech 1974 (=*Protoperidinium spiniferum* (Schiller 1937) Balech 1974, *P. spinosum* Schiller 1937)
1395 *Protoperidinium solitarium* (Abé 1936) Balech 1974
1396 *Protoperidinium somma* (Matzenauer 1933) Balech 1974
1397 *Protoperidinium sourniai* (F.J.R. Taylor 1976) Balech 1994 (non *P. bimucronatum* (Schiller 1937) Balech 1974, *P. bispinum* Schiller 1937)[Balech (1994a)]
1398 *Protoperidinium sphaericum* (Murray *et* Whitting 1899) Balech 1974 (non *P. sphaericum* Okamura 1912, *P. sphaericum* Meunier)
1399 *Protoperidinium sphaeroides* (P. Dangeard 1927) Balech 1974 (=?*Protoperidinium globulus* (Stein 1883) Balech 1974)
1400 *Protoperidinium sphaeroideum* (Mangin 1922) Balech 1974 (=?*P. breve* Paulsen 1907) [Sournia (1978) considered *P. sphaeroides* P. Dangeard and *P. sphaeroideum* Mangin as orthographical variants]
1401 *Protoperidinium spirale* (Gaarder 1954) Balech 1974 (=*P. granii* f. *spirale* Gaarder)
1402 *Protoperidinium spitzbergense* (Broch 1910) Balech 1994 (=*P. spitzbergense* Broch, non *P. globulus* sensu Schiller 1937) [Balech (1994a)]
1403 *Protoperidinium steidingerae* Balech 1979 (=*P. oblongum* (Aurivillus) sec. Steidinger *et* Williams 1970, non *P. oblongum* (Aurivillus) Cleve)
1404 *Protoperidinium steinii* (Jørgensen 1899) Balech 1974 (=*P. michaelis* Stein 1883)
1405 *Protoperidinium stellatum* (Wall 1968) Balech 1994 (=*P. stellatum* (Wall *in* Wall *et* Dale 1968, non *Peridinium compressum* Abé 1981) [Balech (1994a)]
1406 *Protoperidinium subcrassipes* Balech 1988 (=?*P. asymmetricum* Karsten 1907)
1407 *Protoperidinium subcurvipes* (Lebour 1923) Balech 1974 (non *P. subcurvipes* Balech 1959=*Protoperidinium lipopodium* (Balech 1959) Balech 1974)
1408 *Protoperidinium subinerme* (Paulsen 1904) Loeblich III 1970
1409 *Protoperidinium subpyriforme* (P. Dangeard 1927) Balech 1974
1410 *Protoperidinium subsphaericum* (Balech 1959) Balech 1974
1411 *Protoperidinium symmetricum* (Halim 1968) Balech 1974 (non *P. symmetricum* Gaarder 1954)
1412 *Protoperidinium taeningii* (Rampi 1950) Balech 1974
1413 *Protoperidinium tatihouense* (Fauré-Fremiet 1908) Balech 1994 (=*P. minutum* var. *tatihouensis* Fauré-Fremiet 1908) [Balech (1994a)]
1414 *Protoperidinium tenuissimum* (Kofoid 1907) Balech 1974 (=*P. crassiformis* Abé 1981)
1415 *Protoperidinium thorianum* (Paulsen 1905) Balech 1973 (=*P. thorianum* Paulsen, *Properidinium thorianum* Meunier 1919)
1416 *Protoperidinium thulesense* (Balech 1958) Balech 1973 (=*P. conicum* f. *islandica* Braarud 1935, *P. sympholis* Hermosilla *et* Balech 1969)
1417 *Protoperidinium tohrui* Balech 1994 (=*P. paulsenii* Abé 1981) [Balech (1994a)]
**Protoperidinium tregouboffii* (Halim 1955) Balech 1974 (=?*P. brachypus* Schiller 1937, non *P. brachypus* Abé 1981)

Tab. 1. – continued

1418 *Protoperidinium tristylum* (Stein 1883) Balech 1974
1419 *Protoperidinium truncum* (Abé 1936) Balech 1974
1420 *Protoperidinium tuba* (Schiller 1937) Balech 1974
1421 *Protoperidinium tumidum* (Okamura 1907) Balech 1988 (=*P. (divergens) tesselatum* Karsten) [see Balech 1988: 191]
1422 *Protoperidinium turbinatum* (Mangin 1926) Balech 1974
1423 *Protoperidinium turgidum* (Meunier 1910) Balech 1974
1424 *Protoperidinium unipes* (Balech 1962) Balech 1974
1425 *Protoperidinium variegatum* (Peters 1928) Balech 1974
1426 *Protoperidinium ventrale* (Abé 1936) Balech 1974 (=?*P. ventricum* Abé 1927)
1427 *Protoperidinium ventricum* (Abé 1927) Balech 1974 [strongly resembles *P. platifrons*]
1428 *Protoperidinium venustum* (Matzenauer 1933) Balech 1974 (=*P. claudicans* sec Abé 1981)
1429 *Protoperidinium verrucosum* (Meunier 1910) Balech 1974
1430 *Protoperidinium volsella* (Margalef 1968) Balech 1974
1431 *Protoperidinium vulgare* Balech 1978 (=?*P. aliferum* Gaarder *in* Parke *et* Dixon 1968)
1432 *Protoperidinium wiesneri* ssp. *wiesneri* (Schiller 1911) Balech 1988 (=*P. wiesneri* (Schiller) Balech 1974, *P. angustum* (P. Dangeard 1927) Balech 1974, *Protoperidinium wiesneri* ssp. *patagonicum* Balech 1979 (=*P. patagonicum* (Balech 1959) Balech 1974)
1433 *Protoperidinium woloszynskae* (Conrad 1940) Parke *et* Dodge 1976
**Protoperidinium yonedai* (Abé 1981) Balech 1994 [=?*P. latispinum* Mangin 1926] [Balech (1994a)]
1434 *Protoperidinium yserense* (Meunier 1919) Balech 1974

Podolampadaceae Lindemann 1928

98 ***Blepharocysta*** Ehrenberg 1873
1435 *Blepharocysta denticulata* Nie 1939
1436 *Blepharocysta hermosillai* Carbonell-Moore 1992
1437 *Blepharocysta okamurai* Abé 1966 (=?*Blepharocysta splendor-maris* (Ehrenberg 1860) Ehrenberg 1873)
1438 *Blepharocysta paulsenii* Schiller 1937
1439 *Blepharocysta splendor-maris* (Ehrenberg 1860) Ehrenberg 1873 (=?*Blepharocysta okamurai* Abé 1966)
99 ***Gaarderia*** Carbonell-Moore 1994 [genus pre-occupied by the extant coccolithophorid *Gaarderia* (Lecal 1966) Kleijne 1993] [Carbonell-Moore (1994)]

Tab. 1. – continued

1440 *Gaarderia angusta* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1441 *Gaarderia armata* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1442 *Gaarderia compressa* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1443 *Gaarderia lata* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
100 ***Heterobractum*** Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1444 *Heterobractum striatum* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
101 ***Lessardia*** Saldarriaga *et* F.J.R. Taylor 2003 [Saldarriaga *et al.* (2003)] [scarce morphological similarities with Podolampadaceae]
1445 *Lessardia elongata* Saldarriaga *et* F.J.R.Taylor 2003 [Saldarriaga *et al.* (2003)]
102 ***Lissodinium*** Matzenauer 1933 emend. Carbonell-Moore 1991 (18 species)
1446 *Lissodinium australe* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1447 *Lissodinium balechii* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1448 *Lissodinium corrugatum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1449 *Lissodinium fryxelliae* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1450 *Lissodinium heteracanthum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1451 *Lissodinium heteroporum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1452 *Lissodinium homacanthum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1453 *Lissodinium longisulcus* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1454 *Lissodinium magnum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1455 *Lissodinium matzenaueri* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1456 *Lissodinium orcadense* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1457 *Lissodinium ovatum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1458 *Lissodinium parvum* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1459 *Lissodinium schilleri* Matzenauer 1933 (=*Blepharocysta matzenaueri* f. *gibba* Gaarder 1954, *B. matzenaueri* (Matzenauer) Gaarder, *B. compressa* Gaarder 1954)
1460 *Lissodinium steidingerae* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1461 *Lissodinium taylorii* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1462 *Lissodinium thompsonii* Carbonell-Moore 1993 [Carbonell-Moore (1993)]
1463 *Lissodinium zondervanii* Carbonell-Moore 1993 [Carbonell-Moore (1993)]

Tab. 1. – continued

103 ***Mysticella*** Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1464 *Mysticella spinosa* Carbonell-Moore 1994 [Carbonell-Moore (1994)]
1465 *Mysticella striata* (Schütt 1895) Carbonell-Moore 1994 (=*Blepharocysta striata* Schütt) [Carbonell-Moore (1994)]
104 ***Podolampas*** Stein 1883 (7 species)
1466 *Podolampas antarctica* Balech *in* Balech *et* El-Sayed 1965
1467 *Podolampas bipes* Stein 1883
1468 *Podolampas curvata* Schiller 1937
1469 *Podolampas elegans* Schütt 1895
1470 *Podolampas palmipes* Stein 1883
1471 *Podolampas reticulata* Kofoid 1907 (=*P. bipes* var. *reticulata* (Kofoid) F.J.R. Taylor 1976)
1472 *Podolampas spinifera* Okamura 1912
105 ***Roscoffia*** Balech 1956
1473 *Roscoffia capitata* Balech 1956
1474 *Roscoffia minor* Horiguchi *et* Kubo 1997 [Horiguchi and Kubo (1997)]

Pyrophacaceae Lindemann 1928

106 ***Fragilidium*** Balech *ex* Loeblich III 1965 (=***Helgolandicum*** Stosch 1969, ***Goniodoma*** Stein 1883 partim)
1475 *Fragilidium fissile* Balech 1990
1476 *Fragilidium heterolobum* Balech 1959 *ex* Loeblich III 1965
1477 *Fragilidinium lacustre* (Lindemann 1924) Balech 1988 (=*Goniodoma lacustris* Lindemann)
1478 *Fragilidinium mexicanum* Balech 1988
1479 *Fragilidium subglobosum* (Stosch 1969) Loeblich III 1980 (=*Helgolandicum subglobosum* Stosch)
107 ***Pyrophacus*** Stein 1883
1480 *Pyrophacus horologium* Stein 1883 emend. Wall *et* Dale 1971
1481 *Pyrophacus steinii* (Schiller 1935) Wall *et* Dale 1971 (=*P. horologicum* var. *steinii* Schiller 1935, *P. vancampoae* (Rossignol 1962) Wall *et* Dale 1971)

Peridiniales *incertae sedis*

108 ***Adenoides*** Balech 1956
1482 *Adenoides eludens* (Herdman 1922) Balech 1956 (=*Amphidinium eludens* Herdman)

Tab. 1. – continued

1483 *Adenoides kofoidii* (Herdman 1922) Dodge 1982 (=*Amphidinium kofoidii* Herdman, non *Amphidinium kofoidii* var. *petasatum* Herdman 1924)

109 ***Herdmania*** Dodge 1981 [preoccupied]

1484 *Herdmania litoralis* Dodge 1981 emend. Hoppenrath 2000 [=*Gymnodinium agile* Herdman 1922, non *G. agile* Kofoid *et* Swezy 1921][Hoppenrath (2000d)]

Microceratium* Sournia 1972

**Microceratium orstomii* Sournia 1972

110 *Spiraublax* Kofoid 1911 emend. Carbonell-Moore 1996 (=***Gonyaulax*** Diesing 1866 partim) [Carbonell-Moore (1996b)]

1485 *Spiraulax jolliffei* (Murray *et* Whitting 1899) Kofoid 1911 (=*Gonyaulax jolliffei* Murray *et* Whitting, *Spiraulax kofoidii* Graham 1942, *Spiraulaxina kofoidii* (Graham) Loeblich III 1970)

1486 *Spiraulax kofoidii* Graham 1942

Prorocentrales Lemmermann 1910

*Haplodiniaceae Lindemann 1928

Haplodinium* Klebs 1912 [related to *Prorocentrum* according to McLachlan *et al.* (1997)]

**Haplodinium antjoliense* Klebs 1912

**Haplodinium indicum* Subrahmanyan 1966

**Haplodinium iyengaricum* Subrahmanyan 1966

**Haplodinium jonesianum* Subrahmanyan 1966

Prorocentraceae Stein 1883

111 ***Mesoporos*** Lillick 1937 (=*Porella* Schiller 1928)

**Mesoporos parthasarathicus* Subrahmanyan 1966

1487 *Mesoporos perforatus* (Gran 1915) Lillick 1937 (=*Porella adriatica* Schiller 1928, *P. asymmetrica* Schiller 1933, *P. bisimpressa* Schiller 1928, *P. globulus* Schiller 1928, *Mesoporos globulus* (Schiller) Lillick, *Porotheca perforata* (Gran) P.C. Silva 1960)

112 ***Plagiodinium*** Faust *et* Balech 1993

1488 *Plagiodinium belizeanum* Faust *et* Balech 1993 [Faust and Balech (1993)] (the epithet »belizianum« is orthographically correct, ICBN Art. 60.1)

113 ***Prorocentrum*** Ehrenberg 1834 (=***Exuviella*** Cienkowski 1881) (56 species)

1489 *Prorocentrum aporum* (Schiller 1928) Dodge 1975 (=*P. antarcticum* (Hada 1970) Balech 1976, *E. granii* Gaarder 1938)

1490 *Prorocentrum arabianum* Morton *et* Faust 2002 [Morton *et al.* (2002)] (the epithet »arabicum« is orthographically correct, ICBN Art. 60.1)

1491 *Prorocentrum arcuatum* Issel 1928

1492 *Prorocentrum arenarium* Faust 1994 [Faust *et al.* (1994)]

Tab. 1. – continued

1493 *Prorocentrum balticum* (Lohmann 1908) Loeblich III 1970 (=*P. pomoideum* Bursa 1959, ?*E. aequatorialis* Hasle 1960, ?*P. ponticus* Krachmalny *et* Terenko 2002)
1494 *Prorocentrum belizeanum* Faust 1993 [Faust (1993a)] (the epithet »belizianum« is orthographically correct, ICBN Art. 60.1)
1495 *Prorocentrum borbonicum* Ten-Hage, Turquet, Quod, Puiseux-Dao *et* Couté 2000 [Ten-Hage *et al.* (2000b)]
1496 *Prorocentrum caribbaeum* Faust 1993 [Faust (1993a)] (the epithet »caribaeum« is orthographically correct, ICBN Art. 60.1)
1497 *Prorocentrum cassubicum* (Woloszyńska 1928) Dodge 1975
1498 *Prorocentrum clipeus* Hoppenrath 2000 [Hoppenrath (2000a)] (?»clipeum«)
1499 *Prorocentrum compressum* (Bailey 1850) Abé *ex* Dodge 1975 (=*E. oblonga* Schiller 1928, *E. elongata* Rampi 1951, *E. compressa* Ostenfeld 1899, *P. bidens* Schiller 1928, non *P. lenticulatum* (Matzenauer) F.J.R. Taylor 1976, nec *P. lebourae* Schiller 1928]
1500 *Prorocentrum concavum* Fukuyo 1981
1501 *Prorocentrum cordatum* (Ostenfeld 1901) Dodge 1975 [=*E. cordata* Ostenfeld, *E. pyriformis* Schiller 1928, ?*P. minimum* (Pavillard 1916) Schiller 1931]
1502 *Prorocentrum dactylus* (Stein 1883) Dodge 1975 (=*E. dactylus* (Stein) Schütt 1895, *Dinopyxis dactylus* Stein)
1503 *Prorocentrum denatum* Stein 1883 (=?*P. obtusidens* Schiller 1928, ?*P. monacense* Kufferath 1957, non *P. veleoi* Osorio-Tafall 1942, non *P. shikokuense* Hada 1975)
1504 *Prorocentrum elegans* Faust 1993 [Faust (1993a)]
1505 *Prorocentrum emarginatum* Fukuyo 1981
1506 *Prorocentrum faustiae* Morton 1998 [Morton (1998)]
1507 *Prorocentrum foraminosum* Faust 1993 [Faust (1993b)]
1508 *Prorocentrum formosum* Faust 1993 [Faust (1993b)]
1509 *Prorocentrum gracile* Schütt 1895 (=*P. diamantinae* Wood 1963, non *P. sigmoides* Böhm 1933)
1510 *Prorocentrum hoffmannianum* Faust 1990 (=*E. hoffmanniannum* (Faust) McLachlan *et* Boalch 1997) [McLachlan *et al.* (1997), Morton (1998)]
1511 *Prorocentrum lebourae* Schiller 1928 (non *P. compressum* (Bailey 1850) Abé *ex* Dodge 1975)
1512 *Prorocentrum lenticulatum* (Matzenauer 1933) F.J.R. Taylor 1976 (=*E. lenticulata* Matzenauer, non *P. compressum* (Bailey 1850) Abé *ex* Dodge 1975)
1513 *Prorocentrum lima* (Ehrenberg 1860) Dodge 1975 (=*Cryptomonas lima* Ehrenberg 1860, *E. marina* Cienkowski 1881, *E. caspica* Kiselev 1940, *E. lima* (Ehrenberg) Bütschli 1885), *Dinopyxis laevis* Stein 1883, *E. laevis* (Stein) Schröder 1900, *E. chathamensis* Lemmermann 1907, *E. cincta* Schiller 1918, *E. ostenfeldii* Schiller 1931, *Prorocentrum marinum* Dodge *et* Bibby 1973)
1514 *Prorocentrum maculosum* Faust 1993 (=*E. maculosum* (Faust) McLachlan *et* Boalch 1997) [Faust (1993b)]

Tab. 1. – continued

**Prorocentrum magnum* (Gaarder 1954) Dodge 1975

1515 *Prorocentrum maximum* (Gourret 1883) Schiller 1937 (=*P. brochii* Schiller 1918, non *P. mexicanum* Osorio-Tafall 1942)

1516 *Prorocentrum mexicanum* Osorio-Tafall 1942 (non *P. rhathymum* Loeblich III, Sherley *et* R.J. Schmidt 1979)

1517 *Prorocentrum micans* Ehrenberg 1834 (=*P. schilleri* Böhm *in* Schiller 1933, *P. gibbosum* (Schiller 1929) Schiller 1933, *P. levantoides* Bursa 1959, *P. pacificum* Wood 1963)

1518 *Prorocentrum minimum* (Pavillard 1916) Schiller 1931 (=*P. mariae-lebourae* (Parke *et* Ballantine 1957) Loeblich III 1970, *P. triangulatum* Martin 1929, *P. cordiformis* Bursa 1959,?*P. cordatum* (Ostenfeld) Dodge 1975)

1519 *Prorocentrum nanum* Schiller 1918 (non *P. pusillum* (Schiller 1928) Loeblich III 1976) [Puigserver and Zingone (2002)]

1520 *Prorocentrum norrisianum* Faust 1997 [Faust (1997)] (For the epithets commemorating persons, substantive epithets »norrisii« are more commonly applied than adjectival epithets, ICBN Art. 60.11)

1521 *Prorocentrum nux* Puigserver *et* Zingone 2002 [Puigserver and Zingone (2002)]

1522 *Prorocentrum obtusidens* Schiller 1928 (=?*P. dentatum* Stein 1883, *P. shikokuense* sensu Adachi 1972)

1523 *Prorocentrum obtusum* Ostenfeld 1908

1524 *Prorocentrum ovum* (Schiller 1918) Dogde 1975

1525 *Prorocentrum panamense* Grzebyk, Sako *et* Berland 1998 [Grzebyk *et al.* (1998)] (published as »panamensis«, ICBN Art. 23.5 and 32.5)

1526 *Prorocentrum ponticus* Krachmalny *et* Terenko 2002 (=?*P. balticum* (Lohmann 1908) Loeblich III 1970) [Krakhmalny and Terenko (2002)]

1527 *Prorocentrum pusillum* (Schiller 1928) Loeblich III 1976 (=*E. pusilla* Schiller 1928, non *P. nanum* Schiller 1918)

1528 *Prorocentrum rhathymum* Loeblich III, Sherley *et* R.J. Schmidt 1979 (non *P. mexicanum* Osorio-Tafall 1942)

1529 *Prorocentrum redfieldii* Bursa 1959 (=?*P. triestinum* Schiller 1918)

1530 *Prorocentrum reticulatum* Faust 1997 [Faust (1997)]

1531 *Prorocentrum robustum* Osorio-Tafall 1942 (non *P. scutellum* Schröder 1900)

1532 *Prorocentrum rostratum* Stein 1883 (=*P. styliferum* Lohmann 1920, *P. tenue* Lohmann 1920)

1533 *Prorocentrum rotundatum* Schiller 1928 (=*P. cornutum* Schiller 1918)

1534 *Prorocentrum ruetzlerianum* Faust 1990 (For the epithets commemorating persons, substantive epithets »ruetzleri« are more commonly applied than adjectival epithets, Art. 60.11)

1535 *Prorocentrum sabulosum* Faust 1994 [Faust (1994)]

1536 *Prorocentrum sculptile* Faust 1994 [Faust (1994)]

1537 *Prorocentrum scutellum* Schröder 1900 (=*P. sphaeroideum* Schiller 1928, non *P. robustum* Osorio-Tafall 1942)

1538 *Prorocentrum shikokuense* Hada 1975 (=?*P. donghaiense* Lu 2001, non *P. dentatum* Stein 1883) [Lu and Goebel (2001)]

Tab. 1. – continued

1539 *Prorocentrum sigmoides* Böhm 1933 (non *P. gracile* Schütt 1895)

1540 *Prorocentrum triestinum* Schiller 1918 (=*P. setouti* Hada 1975, non *P. shikokuense* Hada 1975,?*P. redfieldii* Bursa 1959, *P. pyrenoideum* Bursa 1959)

1541 *Prorocentrum tropicale* Faust 1997 [Faust (1997)] (published as »tropicalis«, ICBN Art. 23.5 and 32.5)

1542 *Prorocentrum vaginula* (Stein 1883) Dodge 1975 (=*P. adriaticum* Schiller 1918)

1543 *Prorocentrum veloi* Osorio-Tafall 1942 (non *P. dentatum* Stein 1883)

1544 *Prorocentrum venetum* Tolomio *et* Cavolo 1985 (resembles *P. rhathymum* Loeblich III, Sherley *et* R.J. Schmidt / *P. mexicanum* Osorio-Tafall)

Pyrocystales Apstein 1909

Pyrocystaceae (Schütt 1896) Lemmermann 1899

114 ***Dissodinium*** Klebs *in* Pascher 1916 emend. Elbrächter *et* Drebes 1978 (=***Diplodinium*** Klebs 1912, ***Sporodinium*** Gönnert 1936) [a parasite in a part of the life cycle, ?Phytodiniales]

1545 *Dissodinium pseudolunula* E. Swift 1973 *ex* Elbrächter *et* Drebes 1978 (=*D. lunula* (Schütt 1895) Pascher 1976 partim, *Pyrocystis lunula* (Schütt) Schütt 1896 partim, *Gymnodinium lunula* Schütt 1895 partim)

115 ***Pyrocystis*** J. Murray 1876 *ex* Haeckel 1890 (=***Gymnodinium*** Stein 1878 partim, ***Murracystis*** Haeckel 1890, ***Diplodinium*** Klebs 1912, ***Dissodinium*** Klebs *in* Pascher 1916 emend. Elbrächter *et* Drebes 1978 partim) (8 species)

1546 *Pyrocystis acuta* Kofoid 1907

1547 *Pyrocystis apiculata* F.J.R. Taylor 1976

1548 *Pyrocystis elegans* Pavillard 1931

1549 *Pyrocystis fusiformis* (Wyville Thomson 1876 *ex* Haeckel 1890) Blackman 1902 (=*Murracystis fusiformis* Wyville Thomson *in* J. Murray 1885 *ex* Haeckel 1890, *Dissodinium fusiformis* (Thomson *ex* J. Murray) Matzenauer 1933)

**Pyrocystis gerbaultii* Pavillard 1935 (=*Dissodinium gerbaultii* (Pavillard) F.J.R. Taylor 1976

1550 *Pyrocystis hamulus* Cleve 1900

**Pyrocystis lanceolata* Schröder 1900 (=*P. fusiformis* f. *lanceolata* (Schröder) F.J.R. Taylor 1976)

1551 *Pyrocystis lunula* (Schütt 1895) Schütt 1896 (=*Gymnodinium lunula* Schütt 1895, *Diplodinium lunula* (Schütt) Klebs 1912 *in* Pascher 1916, *Dissodinium lunula* (Schütt) F.J.R. Taylor, E. Swift *et* Meunier 1976)

**Pyrocystis margalefii* Léger 1973 (=?*Dissodinium pseudolunula* E. Swift *ex* Elbrächter *et* Drebes 1978)

**Pyrocystis minima* (Matzenauer 1933) Schiller 1937 (=*Dissodinium minimum* Matzenauer)

1552 *Pyrocystis noctiluca* J. Murray 1885 *ex* Haeckel 1890 (=*P. pseudonoctiluca* Wyville Thomson *ex* J. Murray 1876, *P. noctiluca* J. Murray 1885 *ex* Schütt 1896)

Tab. 1. – continued

**Pyrocystis obtusa* Pavillard 1931 (=*Gymnodinium lunula* Schütt 1895)

1553 *Pyrocystis robusta* Kofoid 1907

**Pyrocystis rhomboides* (Matzenauer 1933) Schiller 1937 (=*Dissodinium rhomboides* Matzenauer)

Suessiales Fensome et al. 1993

Suessiaceae Fensome *et al.* 1993

116 ***Polarella*** Montresor, Procaccini *et* Stoecker 1999

1554 *Polarella glacialis* Montresor, Procaccini *et* Stoecker 1999 [Montresor *et al.* (1999)]

Thoracosphaerales Tangen in Tangen et al. 1982

Thoracosphaeraceae Schiller 1930 emend. Tangen *in* Tangen *et al.* 1982

117 ***Thoracosphaera*** Kamptner 1927

1555 *Thoracosphaera heimii* (Lohmann 1920) Kamptner 1944 (=S*yracosphaera heimii* Lohmann)

Dinoflagellates of uncertain classification

****Adinimonas*** Schiller 1928 »Adiniomonas«

**Adinimonas oviforme* Schiller 1928

****Archaeosphaerodiniopsis*** Rampi 1943

**Archaeosphaerodiniopsis verrucosa* Rampi 1943

****Pachydinium*** Pavillard 1915 (=?***Protoceratium*** Bergh 1881,?***Goniodoma*** Stein 1883, non ***Pachydinium*** Kofoid *et* Swezy 1921=***Balechina*** Loeblich Jr. *et* Loeblich III 1968)

**Pachydinium indicum* Matzenauer 1933

**Pachydinium mediterraneum* Pavillard 1915

****Berghiella*** Kofoid *et* Michener 1911

**Berghiella josephinae* F.J.R. Taylor 1976

**Berghiella perplexa* Kofoid 1911

3.1. Diversidad y biogeografía:

3.1.2. Biogeografía

Gómez, F., 2003. Checklist of Mediterranean free-living dinoflagellates. *Botanica Marina* 46, 215-242.

Gómez, F. y Boicenco, L., 2004. An annotated checklist of dinoflagellates in the Black Sea. *Hydrobiologia* 517, 43-59.

Gómez, F., 2006. Endemic and Indo-Pacific plankton in the Mediterranean Sea: A study based on dinoflagellate records. *Journal of Biogeography* 33, 261-270.

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Checklist of Mediterranean Free-living Dinoflagellates

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An annotated checklist of the free-living dinoflagellates (Dinophyceae) of the Mediterranean Sea, based on literature records, is given. The distribution of 673 species in 9 Mediterranean sub-basins is reported. The number of taxa among the sub-basins was as follows: Ligurian (496 species), Balear-Provençal (360), Adriatic (322), Tyrrhenian (284), Ionian (283), Levantine (268), Aegean (182), Alborán (179) and Algerian Seas (151).

Introduction

The oligotrophic conditions in the Mediterranean Sea could favour the richness of dinoflagellates, typical organisms of oligotrophic waters. Intensive studies have been made by Jörgensen (1920, 1923), Schiller (1931–37) (Adriatic Sea), Pavillard (1905–1937) (Gulf of Lions and Monaco), Halim (1960) (Villefranche and Alexandria), Rampi (1939–1969) (Ligurian Sea) and Margalef (1945–1995) (Spanish coasts). However a catalogue of the dinoflagellate species recorded is not available. The aims of this study are to provide a checklist of the species from each sub-basin and to evaluate the species richness of dinoflagellates in the Mediterranean Sea based on a compilation of published data.

Material and Methods

This study is based on literature records of free-living dinoflagellates (Table I), grouped in the main sub-basins of the Mediterranean Sea (Fig. 1). References used for the elaboration of this checklist, but not cited in the text, checklist or notes are listed in the Appendix. Species with their nomenclatural authorities are arranged alphabetically in each order according to the classification proposed by Chrétiennot-Dinet *et al.* (1993) with the following modifications: the genera *Parahistioneis* and *Phalacroma* have been added to the Dinophysaceae; *Balechina* Loeblich *et* Loeblich III, *Plectodinium* Biecheler and the recently erected genera *Akashiwo* G. Hansen *et* Moestrup, *Karenia* G. Hansen *et* Moestrup and *Karlodinium* J. Larsen have been added to the Gymnodiniaceae; *Proterythropsis* Kofoid *et* Swezy *in* Kofoid has been added to the Warnowiaceae; *Pavillardinium* De-Toni has been added to the Oxytoxaceae; *Exuviella* Cienkowski has been added to the Prorocentraceae; *Mysticella* Carbonell-Moore has been added to the Podolampadaceae; *Calcigonellum* Deflandre, *Calcionellum* Defrandre, *Pentapharsodinium* Indelicato *et* Loeblich III and *Preperidinium* Mangin have been added to the Peridiniaceae.

Synonyms have been tracked down and relocated in order to avoid duplicate entries. Synonyms, which have not been quoted in the world literature during the last decades, are not reported. Because of space limitation, not all the references reporting each species for each area have been included. Only when a taxon is reported in less than 3 of the 9 Mediterranean sub-basins considered, is the source of the record reported. Exceptionally, also in 3 of the Mediterranean sub-basins when the number of citations was low (< 5). In some cases, these scarcely reported taxa can be considered as misidentifications or unreliable records, recently described species or rare species. The results of this study depend on the valid identification by the authors of each reference. In most of the cases, there are not photographs or figures of the taxa and the verification of the records is difficult. Records of unarmoured cells should be considered cautiously due to the difficulties of their identification. Most of these doubtful records are in the studies by Skolka *et al.* (1986) for the Libyan waters and/or Innamorati *et al.* (1986, 1989 a,b) for the Ligurian Sea. Many species of the rare genera *Histioneis* and *Heterodinium*, mainly reported by Rampi (1939–1969) and Halim (1960), were not further recorded after their first description. For recently described taxa, the geographical distribution is still unknown beyond the type locality (e.g., some calcareous dinoflagellates). Parasitic (except *Dissodinium pseudolunula* Swift *ex* Elbrächter *et* Drebes) and symbiotic species (i.e., *Symbiodinium* Freudenthal) have been excluded. Freshwater species have been excluded [e.g., *Peridiniella catenata* (Levander) Balech, *P. danica* (Paulsen) Okolodkov *et* Dodge, etc]. Sometimes these species are reported from offshore waters especially in sub-basins such as the Adriatic or Aegean Seas. Taxa only reported from the identification of cysts have been excluded except

Table I. References considered for each Mediterranean sub-basin (references from the Appendix are excluded).

Alb	Arg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev
13	52	4	3	12	21	3	59	1–2
33	56	8–9	6	14–18	149	10	73–74	40
56	87–88	24	19	49	151	20	82–83	46
100	127	34	23	51		22	126	65–66
119		47	27–30	57–58		50		81
		60	32	61–64		71–72		83
		68–69	38–39	75–77		141		85–86
		96–99	54–55	84		150		106–107
		101–105	58	89–93		163–167		126
		115–116	70	116		173–176		
		118	95	125				
		120–122	108–113	129–140				
		168–169	117	160–161				
		171–172	128					
			143–144					
			146–148					
			151					
			162					
			177–178					

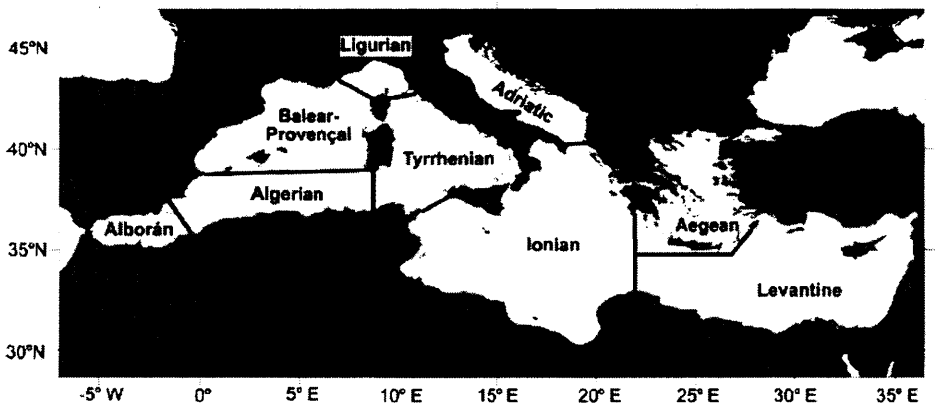

Fig. 1. Map of the Mediterranean sub-basins.

when live cells have germinated from cysts (Ciminiello *et al.* 2000, D'Onofrio *et al.* 1999, Meier *et al.* 2002).

Results

Mediterranean free-living planktonic dinoflagellates were represented by 673 species with 604 and 480 species reported in the western and eastern basins respectively (Table II). The Ligurian (74 %), Balear-Provençal (53 %), Adriatic (48 %), Tyrrhenian = Ionian (42 %) and Levantine (40 %) Seas showed the highest number of species whereas the Aegean (27 %), Alborán (26 %) and Algerian (22 %) Seas showed the lowest number of species.

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Table II. List of taxa and their distribution.

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Actiniscales Sournia 1984										
Actiniscaceae Kützing 1844										
Achradina Lohmann 1903										
Achradina pulchra Lohmann			+		+					76, 116
Actiniscus Ehrenberg 1843										
Actiniscus pentasterias (Ehrenberg) Ehrenberg	+		+	+	+					
Brachydiniales Loeblich III *ex* Sournia 1984										
Brachydiniaceae Sournia 1972										
Asterodinium Sournia 1972										
Asterodinium gracile Sournia[1]				+	+				+	1, 57
Asterodinium libanum Abboud-Abi Saab[1]					+				+	2, 57, 58
Brachydinium F.J.R. Taylor[2]										
Brachydinium capitatum F.J.R. Taylor			+		+		+		+	
Brachydinium taylorii Sournia			+							102
Desmomonadales Pascher 1914										
Desmocapsaceae Pascher 1914										
Desmocapsa Pascher 1914										
Desmocapsa gelatinosa Pascher[3]					+		+			75, 76, 77, 145
Haplodiniaceae Lindemann 1928										
Haplodinium Klebs 1912										
Haplodinium antjoliense Klebs[4]					+					75
Dinococcales Pascher 1914										
Gloeodiniaceae Pascher *ex* Schiller 1937										
Gloeodinium Klebs 1912										
Gloeodinium marinum Bouquaheux[5]			+		+					12, 103, 160
Thoracosphaeraceae Schiller 1930										
Thoracosphaera Kamptner 1927										
Thoracosphaera heimii (Lohmann) Kamptner[6]		+	+	+		+		+	+	
Dinophysales Lindemann 1928										
Citharistaceae Kofoid *et* Skogsberg 1928										
Citharistes Stein 1883										
Citharistes apsteini Schütt									+	81
Citharistes regius Stein				+	+	+				
Dinophysaceae Stein 1883										
Amphisolenia Stein 1883										
Amphisolenia bidentata Schröder	+	+	+	+	+	+	+	+	+	
Amphisolenia bispinosa Kofoid				+						29
Amphisolenia brevicauda Kofoid					+					91, 139
Amphisolenia clavipes Kofoid									+	1, 86
Amphisolenia complanata Kofoid *et* Skogsberg					+					91
Amphisolenia extensa Kofoid	+			+	+					33, 80, 90
Amphisolenia globifera Stein	+	+	+	+	+	+	+	+	+	
Amphisolenia inflata Murray *et* Whitting			+		+					91, 105
Amphisolenia lemmermanni Kofoid									+	40, 46
Amphisolenia palaeotheroides Kofoid					+					91
Amphisolenia palmata Stein			+	+	+		+		+	
Amphisolenia quadrispina Kofoid									+	1, 86
Amphisolenia rectangulata Kofoid			+	+						148, 168
Amphisolenia sigma Halim[7]									+	66
Amphisolenia spinulosa Kofoid		+	+	+	+	+	+		+	
Amphisolenia truncata Kofoid *et* Michener		+	+		+			+	+	
Dinophysis Ehrenberg 1839 (= ***Phalacroma*** Stein 1883 *partim.*)										
Dinophysis acuminata Claparède *et* Lachmann[8]	+	+	+	+	+	+	+	+	+	
Dinophysis acuta Ehrenberg[9]	+	+	+	+	+	+	+	+		
Dinophysis alata Jörgensen[10]			+	+	+	+	+			
Dinophysis amandula (Balech) Sournia[11]		+	+	+	+	+			+	
Dinophysis apicata (Kofoid *et* Skogsberg) Abé *vel* Balech					+					125
Dinophysis apiculata Meunier[12]					+					91
Dinophysis biceps Schiller					+		+			138, 145

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Dinophysis caudata Saville-Kent	+	+	+	+	+	+	+	+	+	
Dinophysis circumsuta (Karsten) Balech			+	+	+	+	+		+	
Dinophysis dentata Schiller					+		+			77, 145, 175
Dinophysis diegensis Kofoid[13]			+		+		+			76, 168, 175
Dinophysis exigua Kofoid *et* Skogsberg									+	81
Dinophysis fortii Pavillard[14]	+		+	+	+	+	+	+	+	
Dinophysis hastata Stein[15]	+		+	+	+	+	+	+	+	
Dinophysis irregularis (Lebour) Balech							+			175
Dinophysis minuta (Cleve) Balech							+			150
Dinophysis mitra (Schütt) Abé *vel* Balech[16]	+		+	+	+	+	+	+	+	
Dinophysis monacantha Kofoid *et* Skogsberg				+						95
Dinophysis ovum Schütt[17]	+	+	+	+	+	+	+	+		
Dinophysis parva Schiller[18]			+		+	+	+			
Dinophysis punctata Jörgensen			+		+	+		+		
Dinophysis pusilla Jörgensen			+		+					76, 115
Dinophysis recurva Kofoid *et* Skogsberg[19]	+		+		+	+	+	+	+	
Dinophysis rete Sournia[20]							+			173, 175
Dinophysis rotundatum Claparède *et* Lachmann	+	+	+	+	+	+	+	+	+	
Dinophysis sacculus Stein[21]	+	+	+	+	+	+	+	+	+	
Dinophysis schilleri Sournia[22]			+	+	+	+	+			
Dinophysis schroederi Pavillard	+		+	+	+	+	+	+		
Dinophysis schuettii Murray *et* Whitting[23]	+		+	+	+	+	+	+	+	
Dinophysis similis Kofoid *et* Skogsberg[24]			+						+	81, 122, 168
Dinophysis sphaerica Stein	+	+	+	+	+	+	+	+	+	
Dinophysis spinosa Rampi		+	+	+	+				+	
Dinophysis tripos Gourret	+	+	+	+	+	+	+	+	+	
Dinophysis uracantha Stein	+		+	+	+	+	+		+	
Histioneis Stein 1883 (= ***Parahistioneis*** Kofoid *et* Skogsberg 1928 *partim.*)										
Histioneis alata Rampi					+					136
Histioneis bernhardii Rampi					+					140
Histioneis cerasus Böhm							+			10
Histioneis depressa Schiller			+		+	+	+			
Histioneis detonii Rampi[25]					+					136
Histioneis elegans Halim					+					64
Histioneis expansa Rampi					+					136
Histioneis faouzii Halim					+					64, 140
Histioneis fragilis Böhm *in* Schiller						+				149
Histioneis gubernans Schütt					+		+			130, 140, 176
Histioneis hippoperoides Kofoid *et* Michener									+	81
Histioneis hyalina Kofoid *et* Michener						+			+	81, 149
Histioneis imbricata Halim					+					64
Histioneis inclinata Kofoid *et* Michener			+		+	+				47, 136, 149
Histioneis isselii Forti					+		+			51, 141
Histioneis joergensenii Schiller			+	+	+	+	+			
Histioneis kofoidii Forti *et* Issel				+			+			50, 95, 141
Histioneis ligustica Rampi					+					133, 136
Histioneis longicollis Kofoid			+		+		+		+	
Histioneis marchesonii Rampi			+		+					34, 133
Histioneis oxypteris Schiller					+		+			140, 145
Histioneis pavillardii Rampi					+					129
Histioneis rampii Halim					+					64
Histioneis remora Stein			+						+	81, 122
Histioneis robusta Rampi					+					140
Histioneis speciosa Rampi					+					140
Histioneis subcarinata Rampi			+		+					99, 136
Histioneis sublongicollis Halim					+					64
Histioneis variabilis Schiller				+	+		+			
Histioneis villafranca Halim					+					64
Histioneis vouckii Schiller					+	+	+			
Ornithocercus Stein 1883										

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Ornithocercus francescae (Murray *et* Whitting) Balech[26]					+		+		+	
Ornithocercus geniculatus Dangeard			+		+				+	
Ornithocercus heteroporus Kofoid	+		+	+	+	+	+		+	
Ornithocercus magnificus Stein	+	+	+	+	+	+	+	+	+	
Ornithocercus quadratus Schütt[27]			+	+	+	+	+	+	+	
Ornithocercus splendidus Schütt[28]			+		+	+			+	
Ornithocercus steinii Schütt *emend.* Kofoid *et* Skogsberg[29]					+		+		+	
Ornithocercus thumii (Schmidt) Kofoid *et* Skogsberg	+		+							33, 115
Parahistioneis Kofoid *et* Skogsberg 1928 (= ***Histioneis*** Stein 1883 *partim.*)										
Parahistioneis acutiformis Rampi					+					136
Parahistioneis karstenii (Kofoid *et* Michener) Kofoid *et* Skogsberg[30]					+					129
Parahistioneis mediterranea Schiller					+	+	+			
Parahistioneis paraformis Kofoid *et* Skogsberg					+				+	81, 136
Parahistioneis sphaeroidea Rampi					+			+		73, 136
Parahistioneis varians Böhm *in* Schiller							+			10
Phalacroma Stein 1883 (= ***Dinophysis*** Ehrenberg 1839 *partim.*)										
Phalacroma acutum (Schütt) Pavillard[31]	+		+		+	+	+			
Phalacroma argus Stein	+	+	+	+	+	+	+		+	
Phalacroma bipartitum Kofoid *et* Skogsberg			+							99
Phalacroma cuneus Schütt		+	+	+	+	+	+		+	
Phalacroma doryphorum Stein	+	+	+	+	+	+	+		+	
Phalacroma expulsum (Kofoid *et* Michener) Kofoid *et* Skogsberg[32]			+		+					64, 69, 99
Phalacroma favus Kofoid *et* Michener			+	+	+	+	+		+	
Phalacroma nasutum Stein[33]	+	+	+	+	+	+				
Phalacroma operculatum Stein	+		+		+		+			
Phalacroma ovatum (Claparède *et* Lachmann) Jörgensen	+	+	+	+	+	+			+	
Phalacroma parvulum (Schütt) Jörgensen	+	+	+	+	+	+	+	+	+	
Phalacroma porodictyum Stein			+	+	+		+		+	
Phalacroma praetextum Kofoid *et* Michener				+						95
Phalacroma pulchellum Lebour	+	+	+	+	+	+		+	+	
Phalacroma striatum Kofoid					+	+	+			80, 125, 173, 175
Triposolenia Kofoid 1906										
Triposolenia bicornis Kofoid			+	+	+	+	+	+		
Triposolenia longicornis Kofoid					+					76
Triposolenia truncata Kofoid	+		+		+		+	+	+	
Oxyphysaceae Sournia 1984										
Oxyphysis Kofoid 1926										
Oxyphysis oxytoxoides Kofoid			+	+			+		+	
Gymnodiniales Lemmermann 1910										
Gymnodiniaceae Lankester 1885										
Akashiwo G. Hansen *et* Moestrup 2000										
Akashiwo sanguinea (Hirasaka) G. Hansen *et* Moestrup[34]		+	+	+	+	+	+	+	+	
Amphidinium Claparède *et* Lachmann 1885										
Amphidinium acutissimum Schiller	+		+		+	+	+			
Amphidinium acutum Lohmann					+	+			+	
Amphidinium carterae Hulburt			+						+	1, 168
Amphidinium conus Schiller					+		+			77, 145
Amphidinium crassum Lohmann[35]		+	+		+	+	+	+		
Amphidinium cucurbitella Kofoid *et* Swezy						+				149
Amphidinium curvatum Schiller					+	+	+			
Amphidinium extensum Wulff					+	+				75, 76, 149
Amphidinium flagellans Schiller					+	+	+			

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Amphidinium glaucum Conrad					+					76
Amphidinium globosum Schröder			+		+	+	+		+	
Amphidinium hyalinum Entz					+	+				77, 149
Amphidinium inflatum Kofoid		+								127
Amphidinium kesslitzi Schiller					+		+		+	
Amphidinium lacustriforme Schiller[36]			+			+	+			
Amphidinium lanceolatum Schröder					+	+	+			
Amphidinium latum Lebour			+			+	+			
Amphidinium lissae Schiller					+		+			76, 77, 175
Amphidinium oceanicum Lohmann					+	+				75, 149
Amphidinium operculatum Claparède *et* Lachmann[37]			+	+			+			145, 177
Amphidinium ovoideum (Lemmermann) Lemmermann					+					76
Amphidinium pellucidum Herdman					+					76
Amphidinium roseolum (Schmarda) Schiller						+				149
Amphidinium schroederi Schiller[38]		+			+	+	+			
Amphidinium sphenoides Wulff[39]					+	+				76, 149
Amphidinium stigmatum Schiller					+	+	+			
Amphidinium turbo Kofoid *et* Swezy					+				+	77, 81
Amphidinium vasculum Kofoid *et* Swezy						+				149
Amphidinium vigrense Woloszynska					+					76
Balechina Loeblich *et* Loeblich III 1966										
Balechina coerulea (Dogiel) F.J.R. Taylor					+	+				76, 149
Balechina marianae F.J.R. Taylor[40]					+					160
Cochlodinium Schütt 1896										
Cochlodinium achromaticum Lebour			+		+					76, 102
Cochlodinium adriaticum Schiller					+		+			77, 145
Cochlodinium brandtii Wulff	+		+		+	+	+			
Cochlodinium citron Kofoid *et* Swezy						+				149
Cochlodinium constrictum (Schütt) Lemmermann				+					+	81, 147
Cochlodinium faurei Kofoid *et* Swezy									+	81
Cochlodinium geminatum (Schütt) Schütt				+						147
Cochlodinium helix (Pouchet) Lemmermann[41]			+			+	+			
Cochlodinium polykrikoides Margalef[42]				+						143
Cochlodinium pulchellum Lebour			+		+		+			
Cochlodinium pupa Lebour			+							101, 102
Cochlodinium strangulatum (Schütt) Schütt				+	+	+				
Cochlodinium turbineum Kofoid *et* Swezy						+				149
Cochodinium schuettii Kofoid *et* Swezy							+			141, 145
Gymnodinium Stein 1878 *emend.* G. Hansen *et* Moestrup										
Gymnodinium achromaticum Lebour			+							34, 99
Gymnodinium agile Kofoid *et* Swezy					+	+				76, 149
Gymnodinium agiliforme Schiller			+		+	+	+			
Gymnodinium albulum Lindemann[43]					+					76
Gymnodinium amphora Kofoid *et* Swezy					+					76
Gymnodinium arcticum Wulff		+			+	+		+		
Gymnodinium attenuatum Kofoid *et* Swezy					+	+				76, 149
Gymnodinium auratum Kofoid *et* Swezy					+	+				76, 149
Gymnodinium aureolum (Hulburt) G. Hansen[44]			+	+		+		+	+	
Gymnodinium aureum Kofoid *et* Swezy			+			+				101, 149
Gymnodinium baccatum Balech			+							34
Gymnodinium biconicum Schiller			+		+	+	+			
Gymnodinium canus Kofoid *et* Swezy						+			+	86, 149
Gymnodinium caput Schiller				+	+	+	+			76, 145, 149
Gymnodinium carinatum Schilling		+								127
Gymnodinium catenatum Graham[45,46]	+	+								13, 56
Gymnodinium cinctum Kofoid *et* Swezy					+					76
Gymnodinium conicum Kofoid *et* Swezy[47]						+	+			22, 149
Gymnodinium corii Schiller				+	+	+	+			
Gymnodinium costatum Kofoid *et* Swezy			+							99

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Gymnodinium cucumis Schütt			+	+	+		+			
Gymnodinium diploconus Schütt				+	+	+				
Gymnodinium dissimile Kofoid *et* Swezy					+	+				76, 149
Gymnodinium elongatum Hope				+		+				144, 149
Gymnodinium flavum Kofoid *et* Swezy					+				+	76, 81
Gymnodinium fulvum Kofoid *et* Swezy						+				149
Gymnodinium fuscum (Ehrenberg) Stein		+			+	+				
Gymnodinium galeaeforme Matzenauer									+	81
Gymnodinium gelbum Kofoid									+	81
Gymnodinium gibberum Schiller				+	+	+	+			
Gymnodinium gleba Schütt				+	+					76, 147
Gymnodinium gracile Bergh						+				149
Gymnodinium grammaticum (Pouchet) Kofoid *et* Swezy[48]				+	+		+		+	
Gymnodinium heterostriatum Kofoid *et* Swezy[49]				+	+	+	+			
Gymnodinium impudicum (Fraga *et* Bravo) G. Hansen *et* Moestrup[46]	+		+	+		+	+		+	
Gymnodinium incertum Herdman					+					76
Gymnodinium incisum Kofoid *et* Swezy					+					76
Gymnodinium lachmannii Saville-Kent					+					75
Gymnodinium lineatum Kofoid *et* Swezy						+				149
Gymnodinium lira Kofoid *et* Swezy					+					76
Gymnodinium lohmannii Paulsen						+			+	40, 149
Gymnodinium maguelonnense Biecheler[50]			+			+				9, 149
Gymnodinium marinum Saville-Kent					+	+			+	
Gymnodinium minor Lebour					+	+	+			21, 22, 76
Gymnodinium mitratum Schiller					+					76
Gymnodinium multilineatum Kofoid *et* Swezy					+					76
Gymnodinium multistriatum Kofoid *et* Swezy			+						+	81, 168
Gymnodinium najadeum Schiller				+	+	+	+			
Gymnodinium nanum Schiller			+		+					75, 76, 77, 102
Gymnodinium neapolitanum Schiller			+	+	+	+	+			
Gymnodinium opressum Conrad			+		+					75, 76, 102
Gymnodinium ostenfeldii Schiller					+		+			75, 76, 145
Gymnodinium ovulum Kofoid *et* Swezy					+					75, 76
Gymnodinium paulsenii Schiller					+	+	+			
Gymnodinium pulchellum J. Larsen[51]			+	+						23, 171
Gymnodinium pulchrum Schiller					+		+			
Gymnodinium punctatum Pouchet					+					75, 76
Gymnodinium pygmaeum Lebour					+					76
Gymnodinium ravenescens Kofoid *et* Swezy					+					76
Gymnodinium rotundatum Klebs		+			+	+	+			
Gymnodinium rubrocinctum Lebour					+					76
Gymnodinium scopulosum Kofoid *et* Swezy					+					76
Gymnodinium semidivisum Schiller					+		+			75, 76, 77, 145
Gymnodinium simplex (Lohmann) Kofoid *et* Swezy[43]			+		+	+	+	+		
Gymnodinium situla Kofoid *et* Swezy						+				149
Gymnodinium sphaericum Calkins						+				149
Gymnodinium sphaeroideum Kofoid					+	+				75, 149
Gymnodinium sulcatum Kofoid *et* Swezy					+					76
Gymnodinium translucens Kofoid *et* Swezy					+					75
Gymnodinium tridentatum Schiller						+				149
Gymnodinium variabile Herdman			+		+	+				75, 76, 77, 102, 149
Gymnodinium vestificii Schütt[52]				+	+					76, 147
Gymnodinium voukii Schiller				+	+	+				
Gymnodinium wulffii Schiller					+	+				77, 149
Gyrodinium Kofoid *et* Swezy 1921 *emend.* G. Hansen *et* Moestrup (= ***Gymnodinium*** Stein 1878 *partim.*)										
Gyrodinium acutum (Schütt) Kofoid *et* Swezy			+	+		+				

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Gyrodinium biconicum Kofoid *et* Swezy						+				149
Gyrodinium conicum Schiller							+			145
Gyrodinium contortum (Schütt) Kofoid *et* Swezy[53]		+		+	+		+		+	
Gyrodinium corsicum Paulmier, Berland, Billard *et* Nezan			+	+	+					
Gyrodinium crassum (Pouchet) Kofoid *et* Swezy			+		+		+			
Gyrodinium cuneatum Kofoid *et* Swezy					+					75
Gyrodinium fissum (Levander) Kofoid *et* Swezy[54]		+								127
Gyrodinium fusiforme Kofoid *et* Swezy	+	+	+		+	+	+	+		
Gyrodinium glaebum Hulburt		+				+			+	
Gyrodinium herbaceum Kofoid *et* Swezy.				+	+	+				
Gyrodinium lachryma (Meunier) Kofoid *et* Swezy[55]		+			+	+	+			
Gyrodinium longum (Lohmann) Kofoid *et* Swezy			+		+					75, 101
Gyrodinium nasutum (Wulff) Schiller						+				149
Gyrodinium ochraceum Kofoid *et* Swezy					+		+			77, 145
Gyrodinium ovatum (Gourret) Kofoid *et* Swezy			+						+	60, 81
Gyrodinium ovum (Schütt) Kofoid *et* Swezy				+			+			144, 145, 147, 166
Gyrodinium parvulum (Schütt) Kofoid *et* Swezy		+		+			+			
Gyrodinium pellucidum (Wulff) Schiller					+	+	+			
Gyrodinium pepo (Schütt) Kofoid *et* Swezy[56]				+		+	+			
Gyrodinium pingue (Schütt) Kofoid *et* Swezy[57]				+	+	+	+			
Gyrodinium rubricaudatum Kofoid *et* Swezy					+					76
Gyrodinium spirale (Bergh) Kofoid *et* Swezy	+		+	+	+		+	+		
Gyrodinium varians (Wulff) Schiller						+	+			
Karenia G. Hansen *et* Moestrup 2000										
Karenia brevis (Davis) G. Hansen *et* Moestrup[58]								+	+	59, 81
Karlodinium J. Larsen 2000										
Karlodinium micrum (Leadbeater *et* Dodge) J. Larsen[59]									+	1
Katodinium Fott 1857 (= ***Massartia*** Conrad 1926)										
Katodinium glaucum (Lebour) Loeblich III[60]					+	+	+			
Katodinium tubulatum (Rampi) Sournia[61]					+					140
Plectodinium Biecheler 1934[62]										
Plectodinium nucleovolvatum Biecheler		+	+		+	+				
Pseliodinium Sournia 1972										
Pseliodinium vaubanii Sournia	+	+	+		+		+		+	
Torodinium Kofoid *et* Swezy 1921										
Torodinium robustum Kofoid *et* Swezy	+		+	+	+	+	+			
Torodinium teredo (Pouchet) Kofoid *et* Swezy[63]			+	+			+		+	2, 118, 145, 146
Polykrikaceae Kofoid *et* Swezy 1921										
Pheopolykrikos Chatton *emend.* Matsuoka *et* Fukuyo 1986										
Pheopolykrikos beauchampii Chatton			+							24
Pheopolykrikos hartmannii (Zimmermann) Matsuoka *et* Fukuyo				+						177
Polykrikos Bütschli 1873										
Polykrikos kofoidii Chatton			+	+		+	+	+		
Polykrikos schwartzii Bütschli	+		+	+	+					
Ptychodiscaceae Lemmermann 1899										
Ptychodiscus Stein 1883										
Ptychodiscus noctiluca Stein[64]			+		+					123, 137
Warnowiaceae Lindemann 1928										
Erythropsidinium P.C. Silva 1960 (= ***Erythropsis*** Hertwig 1884)										
Erythropsidinium agile (Hertwig) P.C. Silva[65]	+			+						33, 147
Erythropsidinium minor (Kofoid *et* Swezy) P.C. Silva			+							101, 102
Erythropsidinium pavillardii (Kofoid *et* Swezy) P.C. Silva[66]			+		+					61, 120
Greuetodinium Loeblich III 1980 (= ***Leucopsis*** Greuet 1968)										

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Greuetodinium cylindricum (Greuet) Loeblich III[67]					+					62
Nematodinium Kofoid *et* Swezy 1921 (= ***Pouchetia*** Schütt 1895)										
Nematodinium armatum (Dogiel) Kofoid *et* Swezy[68]				+	+					38, 76, 93
Nematodinium torpedo Kofoid *et* Swezy			+						+	81, 102
Proterythropsis Kofoid *et* Swezy *in* Kofoid										
Proterythropsis crassicaudata Kofoid *et* Swezy			+							101, 102
Warnowia Lindemann 1928 (= ***Pouchetia*** Schütt)										
Warnowia compacta (Schütt) Schiller				+						147
Warnowia dohrnii Zimmermann			+	+						101, 177
Warnowia fusus (Schütt) Lindemann			+	+	+	+	+			
Warnowia juno (Schütt) Schiller			+	+						101, 147
Warnowia maculata (Kofoid *et* Swezy) Lindemann			+							101
Warnowia polyphemus (Pouchet) Schiller			+			+				120, 149
Warnowia pulchra Schiller				+	+		+			61, 145
Warnowia rosea (Pouchet) Schiller			+		+					49, 121
Warnowia violescens Kofoid *et* Swezy									+	81
Noctilucales Haeckel 1894										
Kofoidiniaceae Taylor 1976										
Cymbodinium Cachon *et* Cachon 1967										
Cymbodinium elegans Cachon *et* Cachon					+					16
Kofoidinium Pavillard 1928										
Kofoidinium pavillardii Cachon *et* Cachon[69]					+					17
Kofoidinium splendens Cachon *et* Cachon					+				+	1, 17
Kofoidinium velelloides Pavillard	+		+	+	+		+	+	+	
Pomatodinium Cachon *et* Cachon 1966										
Pomatodinium impatiens Cachon *et* Cachon			+		+					15, 99
Spatulodinium Cachon *et* Cachon 1968										
Spatulodinium pseudonoctiluca (Pouchet) Cachon *et* Cachon *ex* Loeblich *et* Loeblich III					+		+			18, 173, 175
Leptodiscaceae Kofoid 1916										
Cachonodinium Loeblich III 1980										
Cachonodinium caudatum (Cachon *et* Cachon) Loeblich III[70]					+					18
Craspedotella Kofoid 1905										
Craspedotella pileolus Kofoid					+					17
Leptodiscus Hertwig 1877 (= ***Pratjetella*** Lohmann 1920)										
Leptodiscus medusoides Hertwig[71]			+	+	+					18, 70, 99, 171
Leptophyllus Cachon *et* Cachon 1964 (= ***Abedinium*** Loeblich *et* Loeblich III 1966)										
Leptophyllus dasypus Cachon *et* Cachon[72]					+					14
Petalodinium Cachon *et* Cachon 1969										
Petalodinium porcelio Cachon *et* Cachon					+					18
Scaphodinium Margalef (= ***Leptospathium*** Cachon *et* Cachon 1964)										
Scaphodinium mirabile Margalef[73]	+		+		+				+	
Noctilucaceae Kent 1881										
Noctiluca Suriray *ex* Lamarck 1816										
Noctiluca scintillans (Macartney) Kofoid	+	+	+	+	+	+	+	+	+	
Protodiniferaceae Kofoid *et* Swezy 1921										
Pronoctiluca Fabre-Domergue 1889										
Pronoctiluca pelagica Fabre-Domergue			+		+				+	
Pronoctiluca rostrata F.J.R. Taylor[74]									+	1
Pronoctiluca spinifera (Lohmann) Schiller			+		+			+	+	
Oxyrrhinales Sournia 1984										
Oxyrrhinaceae Sournia 1984										
Oxyrrhis Dujardin 1841										
Oxyrrhis marina Dujardin		+	+	+	+		+			
Peridiniales Haeckel 1894										
Amphidomataceae Sournia 1984										

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Amphidoma Stein 1883 (= ***Pavillardinium*** De-Toni 1936 *partim.*, ***Murrayella*** Kofoid 1907)										
Amphidoma caudata Halldal[75]			+		+		+			
Amphidoma elongata Kofoid *et* Swezy						+				149
Amphidoma nucula Stein[76]	+	+								33, 88
Ceratiaceae Kofoid 1907										
Ceratium Schrank 1793										
Ceratium arietinum Cleve	+	+	+	+	+	+	+	+	+	
Ceratium azoricum Cleve	+	+	+	+	+		+	+		
Ceratium belone Cleve	+	+	+	+	+	+		+	+	
Ceratium breve (Ostenfeld *et* Schmidt) Schröder			+			+		+	+	
Ceratium brunellii Rampi[77]					+					134
Ceratium buceros (Zacharias) Schiller	+	+	+	+	+	+	+	+	+	
Ceratium candelabrum (Ehrenberg) Stein	+	+	+	+	+	+	+	+	+	
Ceratium carriense Gourret	+	+	+	+	+	+	+	+	+	
Ceratium claviger Kofoid[78]	+		+		+					
Ceratium coarctatum Pavillard	+		+	+	+	+		+	+	
Ceratium concilians Jörgensen	+		+	+	+	+	+	+	+	
Ceratium contortum (Gourret) Cleve	+	+	+	+	+	+	+	+	+	
Ceratium contrarium (Gourret) Pavillard[79]	+	+	+	+	+	+	+	+	+	
Ceratium declinatum (Karsten) Jörgensen	+	+	+	+	+	+	+	+	+	
Ceratium deflexum (Kofoid) Jörgensen			+		+		+		+	
Ceratium denticulatum (Jörgensen) Paulsen[80]	+		+					+		82, 119, 168
Ceratium digitatum Schütt			+	+	+	+	+	+	+	
Ceratium egyptiacum Halim[81]									+	1, 65, 86
Ceratium euarcuatum Jörgensen[82]	+	+	+	+	+	+	+	+	+	
Ceratium extensum (Gourret) Cleve[83]	+	+	+	+	+	+	+	+	+	
Ceratium falcatiforme Jörgensen	+		+	+	+				+	
Ceratium falcatum (Kofoid) Jörgensen	+		+	+	+	+	+	+	+	
Ceratium furca (Ehrenberg) Claparède *et* Lachmann	+	+	+	+	+	+	+	+	+	
Ceratium fusus (Ehrenberg) Dujardin	+	+	+	+	+	+	+	+	+	
Ceratium geniculatum (Lemmermann) Cleve	+	+	+		+					
Ceratium gibberum Gourret	+		+	+	+	+	+	+	+	
Ceratium gravidum Gourret	+		+	+	+	+	+	+	+	
Ceratium hexacanthum Gourret	+		+	+	+	+	+	+	+	
Ceratium horridum (Cleve) Gran[84]	+		+	+	+	+	+	+	+	
Ceratium incisum (Karsten) Jörgensen		+	+	+		+	+	+	+	
Ceratium inflatum (Kofoid) Jörgensen		+	+	+	+	+	+	+	+	
Ceratium kofoidii Jörgensen	+		+	+	+	+	+	+	+	
Ceratium limulus (Gourret *ex* Pouchet) Gourret	+	+	+	+	+	+	+	+	+	
Ceratium lineatum (Ehrenberg) Cleve			+	+	+					
Ceratium longirostrum Gourret	+	+	+	+	+	+	+	+	+	
Ceratium longissimum (Schröder) Kofoid			+	+	+	+	+	+	+	
Ceratium lunula (Schimper *ex* Karsten) Jörgensen	+		+	+	+		+		+	
Ceratium macroceros (Ehrenberg) Cleve	+	+	+	+	+	+	+	+	+	
Ceratium massiliense (Gourret) Karsten	+	+	+	+	+	+	+	+	+	
Ceratium minutum Jörgensen			+	+	+				+	
Ceratium paradoxides Cleve[85]	+				+			+	+	
Ceratium pavillardii Jörgensen	+	+	+	+	+	+	+	+	+	
Ceratium pentagonum Gourret	+	+	+	+	+	+	+	+	+	
Ceratium platycorne Daday	+	+	+	+	+	+	+	+	+	
Ceratium praelongum (Lemmermann) Kofoid *ex* Jörgensen	+		+	+	+					
Ceratium pulchellum Schröder	+	+	+	+	+	+	+	+	+	
Ceratium ranipes Cleve	+		+	+	+	+	+	+	+	
Ceratium reflexum Cleve							+			150
Ceratium schroeteri Schröder					+	+	+	+		
Ceratium setaceum Jörgensen	+	+	+	+	+	+	+		+	
Ceratium strictum (Okamura *et* Nishikawa) Kofoid	+		+	+	+		+	+	+	
Ceratium symmetricum Pavillard	+	+	+	+	+	+	+	+	+	
Ceratium tenue (Ostenfeld *et* Schmidt) Jörgensen[86]	+	+	+		+				+	

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Ceratium teres Kofoid	+	+	+	+	+	+	+	+	+	
Ceratium trichoceros (Ehrenberg) Kofoid	+	+	+	+	+	+	+	+	+	
Ceratium tripos (Müller) Schiller	+	+	+	+	+	+	+	+	+	
Ceratium volans Cleve[87]	+		+	+	+	+	+	+	+	
Ceratium vultur Cleve	+		+	+	+	+	+	+	+	
Ceratocorythaceae Lindemann 1928										
Ceratocorys Stein 1883										
Ceratocorys armata (Schütt) Kofoid	+	+	+	+	+	+	+	+	+	
Ceratocorys gourretii Paulsen	+		+	+	+	+	+	+	+	
Ceratocorys horrida Stein	+	+	+	+	+	+	+	+	+	
Cladopyxidaceae Poche 1913										
Cladopyxis Stein 1883 (= ***Micracanthodinium*** Deflandre 1937 *partim.*)										
Cladopyxis brachiolata Stein	+		+	+	+	+	+		+	
Cladopyxis caryophyllum (Kofoid) Pavillard[88]			+	+	+		+		+	
Cladopyxis quadrispina Pavillard[89]	+	+	+		+					
Cladopyxis spinosa (Kofoid) Schiller[90]			+		+					64, 168
Palaeophalacroma Schiller 1928										
Palaeophalacroma unicinctum Schiller[91]			+		+	+	+	+		
Palaeophalacroma verrucosum Schiller					+	+	+			
Crypthecodiniaceae Biecheler *ex* Chatton 1952										
Crypthecodinium Biecheler 1938										
Crypthecodinium cohnii (Seligo) Chatton[92]			+							8
Goniodomataceae Lindemann 1928										
Goniodoma Stein 1883 (= ***Triadinium*** Dodge 1981, = ***Heteraulacus*** Diesing 1850 *partim.*)										
Goniodoma acuminatum (Ehrenberg) Stein[93]	+	+	+	+	+	+	+	+	+	
Goniodoma sphaericum Murray *et* Whitting[94]	+	+	+		+		+	+	+	
Pyrodinium Plate 1906										
Pyrodinium bahamense Plate[95]									+	40
Gonyaulacaceae Lindemann 1928										
Alexandrium Halim *emend.* Balech 1989 (= ***Protogonyaulax*** F.J.R. Taylor 1976)										
Alexandrium andersonii Balech				+						27
Alexandrium balechii (Steidinger) Balech				+				+		110, 156
Alexandrium catenella (Whedon *et* Kofoid) Balech	+		+	+					+	
Alexandrium compressum (Fukuyo, Yoshida *et* Inoue) Balech							+			20
Alexandrium concavum (Gaarder) Balech				+						30
Alexandrium foedum Balech				+						6, 30
Alexandrium insuetum Balech				+						30
Alexandrium kutnerae (Balech) Balech				+						30
Alexandrium leei Balech			+	+						30
Alexandrium margalefii Balech			+	+						30
Alexandrium minutum Halim[96]			+	+		+	+	+	+	
Alexandrium ostenfeldii (Paulsen) Balech *et* Tangen[97]		+							+	87, 107
Alexandrium pseudogonyaulax (Biecheler) Horiguchi *ex* Kita *et* Fukuyo			+	+			+			20, 30, 71
Alexandrium tamarense (Lebour) Balech			+	+	+	+	+	+	+	
Alexandrium taylorii Balech			+	+		+				
Amylax Meunier 1910 (= ***Gonyaulax*** Diesing 1866 *partim.*)										
Amylax buxus (Balech) Dodge[98]									+	1
Amylax triacantha (Jörgensen) Sournia[99]		+								87
Gonyaulax Diesing 1866 (= ***Amylax*** Meunier 1910 *partim.*)										
Gonyaulax africana Schiller			+	+	+					76, 138, 145
Gonyaulax birostris Stein			+	+	+	+	+	+	+	
Gonyaulax brevisulcatum Dangeard	+				+					33, 76, 100, 119
Gonyaulax diegensis Kofoid[100]		+	+		+	+		+	+	
Gonyaulax digitale (Pouchet) Kofoid[101]	+	+	+	+	+	+	+	+	+	

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Gonyaulax elegans Rampi					+					138
Gonyaulax fragilis (Schütt) Kofoid	+		+	+	+	+	+			
Gonyaulax glyptorhynchus Murray *et* Whitting[102]				+						95
Gonyaulax gracilis Schiller		+					+			52, 167
Gonyaulax highleyii Murray *et* Whitting[103]										114
Gonyaulax hyalina Ostenfeld *et* Schmidt					+		+			138, 173, 174, 175
Gonyaulax ligustica Rampi			+		+					118, 138
Gonyaulax kofoidii Pavillard[104]		+		+	+	+	+	+	+	
Gonyaulax minuta Kofoid *et* Michener[105]			+	+	+		+		+	
Gonyaulax monacantha Pavillard	+	+	+	+	+	+	+	+	+	
Gonyaulax monospina Rampi					+		+			20, 138, 167
Gonyaulax orientalis Lindemann					+					76
Gonyaulax ovalis Schiller[106]			+	+	+		+			
Gonyaulax pacifica Kofoid[104, 107]	+	+	+	+	+	+	+		+	
Gonyaulax polygramma Stein	+	+	+	+	+	+	+	+	+	
Gonyaulax rostrata Dangeard			+							168
Gonyaulax rotundata Rampi					+		+			22, 138
Gonyaulax rugosum Wailes[103]						+				114, 149
Gonyaulax scrippsae Kofoid			+	+	+	+			+	
Gonyaulax sphaeroidea Kofoid					+					135
Gonyaulax spinifera (Claparède *et* Lachmann) Diesing[108]	+	+	+	+	+	+	+	+	+	
Gonyaulax trottii Rampi					+					138
Gonyaulax turbynei Murray *et* Whitting			+		+		+	+	+	
Gonyaulax unicornis Lebour					+					64, 76
Gonyaulax verior Sournia[109]		+	+	+	+		+	+	+	
Lingulodinium Wall *emend.* Dodge 1989										
Lingulodinium milneri (Murray *et* Whitting) Dodge[110]									+	86
Lingulodinium polyedra (Stein) Dodge[111]	+	+	+	+	+	+	+	+	+	
Protoceratium Bergh 1881 (= ***Gonyaulax*** Diesing 1866 *partim.*)										
Protoceratium areolatum Kofoid	+		+		+			+		
Protoceratium pepo Kofoid *et* Michener					+					138
Protoceratium reticulatum (Claparède *et* Lachmann) Bütschli[112]	+	+	+	+	+	+	+	+	+	
Protoceratium spinulosum (Murray *et* Whitting) Schiller		+	+		+					
Heterodiniaceae Lindemann 1928										
Heterodinium Kofoid 1906										
Heterodinium agassizii Kofoid					+					125
Heterodinium balechii Rampi			+		+					138, 168
Heterodinium crassipes Schiller							+			145
Heterodinium debeauxii Rampi					+					131
Heterodinium dispar Kofoid *et* Adamson			+		+					34, 99, 138
Heterodinium doma (Murray *et* Whitting) Kofoid					+					131
Heterodinium dubium Rampi					+					131
Heterodinium fides Kofoid									+	1
Heterodinium globosum Kofoid					+					124, 125, 131
Heterodinium grahamii Rampi					+					64, 138
Heterodinium inaequale Kofoid[113]			+		+					64, 121
Heterodinium kofoidii Pavillard			+		+		+			90, 122, 145
Heterodinium laticeps Léger					+					90
Heterodinium leiorhynchum (Murray *et* Whitting) Kofoid			+	+	+				+	
Heterodinium mediterraneum Pavillard			+		+	+			+	
Heterodinium milneri (Murray *et* Whitting) Kofoid			+		+		+			64, 124, 129, 175
Heterodinium minutum Kofoid *et* Michener			+						+	34, 81
Heterodinium murrayi Kofoid					+					49, 64, 131, 139
Heterodinium rigdenae Kofoid									+	1

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Heterodinium scrippsi Kofoid[114]			+		+		+			64, 89, 90, 91, 124, 175
Heterodinium sinistrum Kofoid *et* Adamson[115]									+	1
Heterodinium whittingae Kofoid					+					91, 92, 124, 125, 139
Ostreopsidaceae Lindemann 1928										
Coolia Meunier 1919 (= ***Ostreopsis*** J. Schmidt 1901 *partim.*)										
Coolia monotis Meunier[116]			+	+	+		+			
Ostreopsis J. Schmidt 1901										
Ostreopsis ovata Fukuyo				+						162
Ostreopsis siamensis J. Schmidt				+	+					151, 161
Oxytoxaceae Lindemann 1928										
Centrodinium Kofoid 1907 (= ***Pavillardinium*** De-Toni 1936 *partim.*, ***Murrayella*** Kofoid 1907 *partim.*)										
Centrodinium biconicum (Murray *et* Whitting) F.J.R. Taylor[117]					+				+	81, 138
Centrodinium complanatum (Cleve) Kofoid			+		+				+	
Centrodinium elongatum Kofoid	+									33
Centrodinium eminens Böhm					+		+			91, 138, 175
Centrodinium intermedium Pavillard			+		+	+				
Centrodinium maximum Pavillard	+		+		+				+	
Centrodinium pavillardii F.J.R. Taylor[118]	+		+	+	+			+	+	
Centrodinium splendidum (Rampi) F.J.R. Taylor[119]					+					131, 138
Corythodinium Loeblich *et* Loeblich III 1966 (= ***Oxytoxum*** Stein 1883 *partim.*)										
Corythodinium belgicae (Meunier) F.J.R. Taylor[103]					+				+	76, 81, 114
Corythodinium compressum (Kofoid) F.J.R. Taylor	+		+		+					
Corythodinium constrictum (Stein) F.J.R. Taylor	+	+	+	+	+	+	+	+	+	
Corythodinium cristatum (Kofoid) F.J.R. Taylor			+		+	+				
Corythodinium curvicaudatum (Kofoid) F.J.R. Taylor			+							168
Corythodinium diploconus (Stein) F.J.R. Taylor		+			+		+			64, 88, 175
Corythodinium elegans (Pavillard) F.J.R. Taylor			+	+	+	+			+	
Corythodinium frenguellii (Rampi) F.J.R. Taylor			+		+		+			138, 168, 175
Corythodinium reticulatum (Stein) Loeblich *et* Loeblich III		+	+	+	+	+	+	+	+	
Corythodinium tessellatum (Stein) Loeblich *et* Loeblich III	+	+	+	+	+	+	+	+	+	
Oxytoxum Stein 1883										
Oxytoxum aceratum Rampi					+					138
Oxytoxum adriaticum Schiller				+	+	+	+			
Oxytoxum areolatum Rampi			+		+		+			22, 68, 131
Oxytoxum brunellii Rampi[120]			+		+			+		64, 74, 118, 138
Oxytoxum caudatum Schiller			+		+	+	+			
Oxytoxum coronatum Schiller					+	+	+			140, 145, 175
Oxytoxum crassum Schiller			+		+		+	+		
Oxytoxum cribosum Stein					+					140
Oxytoxum curvatum (Kofoid) Kofoid[121]			+		+	+			+	
Oxytoxum depressum Schiller			+		+		+	+		
Oxytoxum elongatum Wood									+	81
Oxytoxum gladiolus Stein		+			+	+	+	+		
Oxytoxum globosum Schiller[122]				+	+	+	+			
Oxytoxum laticeps Schiller			+		+	+	+		+	
Oxytoxum longiceps Schiller[123]	+		+	+	+	+	+	+	+	
Oxytoxum longum Schiller	+		+		+		+			
Oxytoxum milneri Murray *et* Whitting[124]	+		+	+	+	+	+		+	
Oxytoxum minutum Rampi			+	+	+	+	+			
Oxytoxum obesum Rampi					+					140
Oxytoxum obliquum Schiller					+	+	+			
Oxytoxum ovale Schiller[125]	+		+	+	+	+	+	+		
Oxytoxum pachyderme Schiller *ex* F.J.R. Taylor							+			145

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Oxytoxum parvum Schiller[126]			+		+	+	+	+		
Oxytoxum punctulatum Rampi[127]				+	+					55, 138
Oxytoxum radiosum Rampi					+					131, 138
Oxytoxum rampii Sournia[128]				+	+					29, 140
Oxytoxum scolopax Stein	+	+	+	+	+	+	+	+	+	
Oxytoxum sphaeroideum Stein		+	+		+	+	+	+	+	
Oxytoxum spinosum Rampi					+					64, 131
Oxytoxum subulatum Kofoid			+	+	+					29, 91, 105
Oxytoxum turbo Kofoid					+	+			+	
Oxytoxum variabile Schiller[129]	+		+	+	+	+	+		+	
Oxytoxum viride Schiller				+	+	+	+		+	
Pavillardinium De-Toni 1936 (= ***Amphidoma*** Stein 1883 *partim.*, ***Murrayella*** Kofoid 1907)										
Pavillardinium ovale (Pavillard) De-Toni[130]				+						29, 123
Schuettiella Balech 1988 (= ***Gonyaulax*** Diesing 1866 *partim.*, ***Oxytoxum*** Stein 1883 *partim.*)										
Schuettiella mitra (Schütt) Balech[131]	+	+	+	+	+	+	+			
Peridiniaceae Ehrenberg 1828										
Calcigonellum Deflandre 1948										
Calcigonellum infula Deflandre *emend.* Montresor[132]				+						39
Calciodinellum Deflandre 1947										
Calciodinellum levantinum Meier, Janofske *et* Willems[133]									+	106
Calciodinellum operosum Deflandre[132]				+						39
Diplopelta Stein *ex* Jörgensen 1912 (= ***Dissodium*** Abé 1941 *partim.*)										
Diplopelta bomba Stein *ex* Jörgensen[134]	+		+	+	+				+	
Diplopelta symmetrica Pavillard[135]			+	+	+					
Diplopsalis Bergh 1881 (= ***Dissodium*** Abé 1941 *partim.*)										
Diplopsalis lenticula Bergh[136]	+	+	+	+	+	+	+	+	+	
Diplopsalopsis Meunier *emend.* Balech 1988										
Diplopsalopsis orbicularis (Paulsen) Meunier[137]							+			150
Diplopsalopsis latipeltata Balech *et* Borgese				+						28, 144
Kryptoperidinium Lindemann 1924 (= ***Glenodinium*** Ehrenberg 1837 *partim.*)										
Kryptoperidinium foliaceum (Stein) Lindemann[138]			+			+		+		
Oblea Balech *ex* Loeblich *et* Loeblich III 1966										
Oblea rotunda (Balech) Balech *ex* Sournia[139]				+		+				32, 149
Pentapharsodinium Indelicato *et* Loeblich III 1986 (= ***Peridinium*** Ehrenberg 1831 *partim.*)										
Pentapharsodinium tyrrhenicum (Balech) Montresor, Zingone *et* Marino[140]				+						6, 111
Peridinium Ehrenberg 1831[141]										
Peridinium quinquecorne Abé[142]				+			+		+	
Preperidinium Mangin 1913 (= ***Diplopeltopsis*** Pavillard 1913, ***Zygabikodinium*** Loeblich *et* Loeblich III 1970)										
Preperidinium meunieri (Pavillard) Elbrächter[143]			+	+	+				+	
Protoperidinium Bergh *emend.* Balech 1974[141] (= ***Peridinium*** Ehrenberg 1831 *partim.*, ***Minuscula*** Lebour 1925)										
Protoperidinium abei (Paulsen) Balech[144]	+		+	+	+			+	+	
Protoperidinium anthonyi (Fauré-Fremiet) Balech					+					76
Protoperidinium bipes (Paulsen) Balech[145]	+	+	+		+	+	+	+		
Protoperidinium bispinum (Schiller) Balech[146]		+		+	+		+	+		
Protoperidinium brevipes (Paulsen) Balech							+	+	+	
Protoperidinium brochii (Kofoid *et* Swezy) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium bulla (Meunier) Balech					+					76
Protoperidinium cerasus (Paulsen) Balech	+	+	+		+	+	+	+	+	
Protoperidinium claudicans (Paulsen) Balech	+	+	+	+	+			+	+	

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Protoperidinium conicoides (Paulsen) Balech									+	40
Protoperidinium conicum (Gran) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium crassipes (Kofoid) Balech[147]		+	+	+	+	+	+	+	+	
Protoperidinium curvipes (Ostenfeld) Balech[148]	+	+			+		+		+	
Protoperidinium deficiens (Meunier) Balech									+	86
Protoperidinium depressum (Bailey) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium diabolus (Cleve) Balech[149]	+	+	+	+	+	+	+	+	+	
Protoperidinium divergens (Ehrenberg) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium elegans (Cleve) Balech			+		+		+			
Protoperidinium excentricum (Paulsen) Balech			+		+			+		
Protoperidinium exiguipes (Mangin *ex* Halim) Dodge									+	40
Protoperidinium fimbriatum (Meunier) Balech					+					76
Protoperidinium finitimum Balech[150]			+	+	+			+	+	
Protoperidinium globulus (Stein) Balech[151]	+	+	+	+	+	+	+	+	+	
Protoperidinium grande (Kofoid) Balech	+	+	+		+		+	+	+	
Protoperidinium granii (Ostenfeld) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium heteracanthum (Dangeard) Balech			+		+					77, 99
Protoperidinium hirobis (Abé) Balech				+					+	1, 144
Protoperidinium inclinatum (Balech) Balech			+							99
Protoperidinium inflatum (Okamura) Balech	+		+	+	+	+			+	
Protoperidinium latispinum (Mangin) Balech	+		+		+				+	
Protoperidinium leonis (Pavillard) Balech	+	+	+	+	+		+	+	+	
Protoperidinium ligusticum (Rampi) Balech					+					138
Protoperidinium maranense Tolomio							+			163, 165
Protoperidinium marielebourae (Paulsen) Balech	+		+	+	+		+			
Protoperidinium mediterraneum (Kofoid) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium minutum (Kofoid) Loeblich III	+	+			+			+	+	
Protoperidinium mite (Pavillard) Balech	+		+		+		+		+	
Protoperidinium nipponicum (Abé) Balech[152]							+		+	40, 150
Protoperidinium nudum (Meunier) Balech[153]			+							98, 99
Protoperidinium oblongum (Aurivillius) Parke *et* Dodge	+		+	+	+		+		+	
Protoperidinium obtusum (Karsten) Parke *et* Dodge							+			150
Protoperidinium oceanicum (Vanhöffen) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium oviforme (Dangeard) Balech	+	+	+		+					
Protoperidinium ovum (Schiller) Balech		+	+	+	+	+	+		+	
Protoperidinium pallidum (Ostenfeld) Balech	+	+	+	+	+		+	+	+	
Protoperidinium parthenopes Zingone *et* Montresor				+						178
Protoperidinium pedunculatum (Schütt) Balech		+	+		+		+	+	+	
Protoperidinium pellucidum (Schütt) Balech	+	+	+	+	+		+	+	+	
Protoperidinium pentagonum (Gran) Balech	+	+	+	+		+	+	+	+	
Protoperidinium punctulatum (Paulsen) Balech	+		+	+	+		+	+	+	
Protoperidinium pyriforme (Paulsen) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium quarnerense (Schröder) Balech	+		+	+	+		+	+	+	
Protoperidinium schilleri (Paulsen) Balech	+		+		+					
Protoperidinium simulum (Paulsen) Balech	+		+		+				+	
Protoperidinium sinaicum (Matzenauer) Balech					+	+				76, 77, 149
Protoperidinium solidicorne (Mangin) Balech[154]			+	+	+		+		+	
Protoperidinium sphaericum (Murray *et* Whitting) Balech			+	+	+	+	+		+	
Protoperidinium sphaeroides (Dangeard) Balech[155]	+		+		+					
Protoperidinium sphaeroideum (Mangin) Balech[155]						+				149
Protoperidinium steinii (Jörgensen) Balech	+	+	+	+	+	+	+	+	+	
Protoperidinium subinerme (Paulsen) Loeblich III	+		+	+	+		+	+	+	
Protoperidinium thorianum (Paulsen) Balech	+				+	+			+	
Protoperidinium tregouboffii (Halim) Balech[156]					+					63, 64
Protoperidinium tristylum (Stein) Balech			+		+		+			76, 168, 175
Protoperidinium tubum (Schiller) Balech	+		+		+		+			
Protoperidinium tumidum (Okamura) Balech		+			+		+			
Protoperidinium variegatum (Peters) Balech		+								127
Protoperidinium wiesneri (Schiller) Balech[157]			+		+		+			

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Scrippsiella Balech *ex* Loeblich III 1965[158]										
Scrippsiella lachrymosa Lewis				+						39, 112
Scrippsiella precaria Montresor *et* Zingone				+						109
Scrippsiella ramonii Montresor				+						39, 108
Scrippsiella rotunda Lewis				+						39, 117
Scrippsiella spinifera Honsell *et* Cabrini							+			72
Scrippsiella trochoidea (Stein) Balech *ex* Loeblich III[159]	+	+	+	+	+	+	+	+	+	
Podolampadaceae Lindemann 1928										
Blepharocysta Ehrenberg 1873										
Blepharocysta hermosillai Carbonell-Moore				+						19
Blepharocysta paulsenii Schiller			+		+	+			+	
Blepharocysta splendor-maris (Ehrenberg) Stein	+	+	+		+				+	
Mysticella Carbonell-Moore 1994										
Mysticella striata (Schütt) Carbonell-Moore[160]					+					132
Podolampas Stein 1883										
Podolampas bipes Stein	+	+	+	+	+	+	+	+	+	
Podolampas curvatus Schiller					+		+			76, 145
Podolampas elegans Schütt	+	+	+	+	+	+	+	+	+	
Podolampas palmipes Stein	+	+	+	+	+	+	+	+	+	
Podolampas spinifera Okamura[161]	+	+	+	+	+	+	+	+	+	
Pyrophacaceae Lindemann 1928										
Pyrophacus Stein 1883										
Pyrophacus horologium Stein *emend.* Wall *et* Dale	+	+	+	+	+	+	+	+	+	
Pyrophacus steinii (Schiller) Wall *et* Dale			+	+	+		+	+	+	
Pyrophacus vancampoae (Rossignol) Wall *et* Dale[162]			+							96, 160
Peridiniales *incertae sedis*										
Ceratoperidinium Margalef *ex* Loeblich III 1980										
Ceratoperidinium mediterraneum Abboud-Abi Saab[163]									+	2
Ceratoperidinium yeye Margalef *ex* Loeblich III[163]			+						+	1, 99, 169
Fragilidium Balech *ex* Loeblich III 1965 (= ***Helgolandicum*** von Stosch 1869, ***Goniodoma*** Stein 1883 *partim.*)										
Fragilidium fissile Balech				+						6
Heterocapsa Stein 1883 (= ***Cachonina*** Loeblich III 1968)										
Heterocapsa lanceolata Iwataki *et* Fukuyo[164]								+		126
Heterocapsa niei (Loeblich III) Morrill *et* Loeblich III[165]				+		+	+			
Heterocapsa rotundata (Lohmann) G. Hansen[166]		+			+			+	+	
Heterocapsa triquetra (Ehrenberg) Stein		+	+			+	+	+		
Micracanthodinium Deflandre 1937 (= ***Cladopyxis*** Stein 1883 *partim.*)										
Micracanthodinium bacilliferum (Schiller) Deflandre[167]					+		+			20, 140
Micracanthodinium claytonii (Holmes) Dodge[168]					+		+			22, 140
Micracanthodinium setiferum (Lohmann) Deflandre[169]			+	+	+	+	+			
Spiraulax Kofoid 1911 (= ***Gonyaulax*** Diesing 1866 *partim.*)										
Spiraulax jolliffei (Murray *et* Whitting) Kofoid	+		+	+	+		+	+	+	
Prorocentrales Lemmermann 1910										
Prorocentraceae Stein 1883										
Exuviella Cienkowski 1881[170]										
Exuviella aperta Schiller[171]			+		+		+			77, 145, 168
Mesoporos Lillick 1937 (= ***Porella*** Schiller 1928)										
Mesoporos globulus (Schiller) Lillick		+	+	+	+	+	+			
Mesoporos perforatus (Gran) Lillick	+	+	+	+	+	+	+	+	+	
Prorocentrum Ehrenberg 1834[170] (= ***Exuviella*** Cienkowski 1881)										
Prorocentrum aporum (Schiller) Dodge	+		+	+	+	+	+	+		
Prorocentrum arcuatum Issel[172]			+	+	+		+	+		

Table II. (continued)

Dinophyceae West *et* Fritsch 1927	Alb	Alg	Bal	Tyr	Lig	Ion	Adr	Aeg	Lev	Reference no.
Prorocentrum balticum (Lohmann) Loeblich III	+		+		+	+	+	+	+	
Prorocentrum belizeanum Faust				+		+				151
Prorocentrum cassubicum (Woloszynska) Dodge					+			+		75, 76, 83
Prorocentrum compressum (Bailey) Abé *ex* Dodge[173]	+	+	+	+	+	+	+	+	+	
Prorocentrum concavum Fukuyo				+		+				151
Prorocentrum cordatum (Ostenfeld) Dodge[174,175]	+		+		+	+	+	+	+	
Prorocentrum dactylus (Stein) Dodge		+	+		+	+	+			
Prorocentrum dentatum Stein[176]	+		+	+	+	+	+	+	+	
Prorocentrum emarginatum Fukuyo			+							172
Prorocentrum gracile Schütt[177]		+	+	+	+	+	+	+		
Prorocentrum lima (Ehrenberg) Dodge		+	+	+	+	+	+	+		
Prorocentrum maximum (Gourret) Schiller[178]			+	+	+	+	+			
Prorocentrum micans Ehrenberg[179]	+	+	+	+	+	+	+	+	+	
Prorocentrum minimum (Pavillard) Schiller[175]			+	+	+	+	+	+		
Prorocentrum nanum Schiller[180]			+		+		+			
Prorocentrum nux Puigserver *et* Zingone				+						128
Prorocentrum ovum (Schiller) Dogde			+	+	+		+	+		
Prorocentrum rostratum Stein	+		+		+			+	+	
Prorocentrum rotundatum Schiller[181]		+	+	+	+	+	+	+	+	
Prorocentrum scutellum Schröder[182]	+	+	+	+	+	+	+	+	+	
Prorocentrum triestinum Schiller		+	+	+	+	+	+	+	+	
Prorocentrum vaginulum (Stein) Dodge[183]		+	+		+	+	+	+	+	
Prorocentrum venetum Tolomio *et* Cavolo[184]							+			164
Protaspidales Loeblich III 1970										
Entomosigmataceae Chatton 1952										
Entomosigma Schiller 1925										
Entomosigma peridinioides Schiller[185]				+	+		+			75, 76, 145
Pyrocystales Apstein 1909										
Pyrocystaceae (Schütt) Lemmermann 1899										
Dissodinium Klebs *in* Pascher *emend.* Elbrächter *et* Drebes 1978[186]										
Dissodinium pseudolunula Swift *ex* Elbrächter *et* Drebes[187]			+	+	+	+	+	+	+	
Pyrocystis Murray *ex* Haeckel 1890[186] (= ***Gymnodinium*** Stein 1883 *partim.*, ***Dissodinium*** Klebs *in* Pascher *emend.* Elbrächter *et* Drebes 1978 *partim.*)										
Pyrocystis acuta Kofoid					+					76, 125
Pyrocystis elegans Pavillard	+		+	+	+	+	+	+	+	
Pyrocystis fusiformis (Wyville-Thomson *ex* Haeckel) Blackman[188]	+		+	+	+	+	+	+	+	
Pyrocystis gerbaultii Pavillard[189]			+	+	+					
Pyrocystis hamulus Cleve			+		+	+	+		+	
Pyrocystis margalefii Léger[190]			+		+					91, 104
Pyrocystis minima (Matzenauer) Schiller[191]				+	+	+	+			
Pyrocystis noctiluca Murray *ex* Schütt[192]		+	+	+	+		+		+	
Pyrocystis obtusa Pavillard			+	+	+	+	+	+	+	
Pyrocystis robusta Kofoid			+	+	+	+	+		+	
Dinoflagellates of uncertain identification										
Adinimonas Schiller 1928										
Adinimonas oviforme Schiller[193]		+				+	+		+	
Archaeosphaerodiniopsis Rampi 1943										
Archaeosphaerodiniopsis verrucosa Rampi[194]					+					135
Pachydinium Pavillard 1915										
Pachydinium mediterraneum Pavillard[195]			+		+	+				

Notes

[1] Reported in the Western Mediterranean Sea by Gómez and Claustre (2003). These records assigned to *Asterodinium gracile* Sournia presented morphological differences with respect the type species. *Asterodinium libanum* Abboud-Abi Saab requires a more detailed description.

[2] The type species *Brachydinium capitatum* F.J.R. Taylor (Taylor 1963) was replaced by *Brachidinium capitatum* F.J.R. Taylor due to an etymological error (Taylor 1967). Sournia (1973 p. 5) reported that the correction is invalid.

[3] Rare dinoflagellate epiphytic on Rhodophyceae (see Sournia 1986, p. 36).

[4] Rare and insufficiently described taxon (Sournia 1986, p. 36).

[5] According to Taylor (1976 p. 190), the cysts were reported by Margalef *et al.* (1954). *Gloeodinium* Klebs and *Hemidinium* Stein have been considered as the immobile and mobile stage respectively of the life cycle of the same taxa (see Sournia 1986 p. 67). The continental species, *Hemidinium nasutum* Stein and others, are reported in the Mediterranean waters (e.g., Schiller 1935–1937, p. 89–92, Viličić *et al.* 2002).

[6] *Syracosphaera heimii* Lohmann. This taxon was previously considered to be a coccolithophorid and has been scarcely reported in dinoflagellate checklists (see Tangen *et al.* 1982).

[7] This taxon resembles *Amphisolenia spinulosa* Kofoid and *Amphisolenia mozambica* Sournia.

[8] This taxon presents synonyms as *Dinophysis borealis* Paulsen, *D. lachmanni* Paulsen, *D. boehmii* Paulsen or *D. skagii* Paulsen.

[9] *Dinophysis dens* Pavillard.

[10] The orthographical similarity of *Dinophysis alata* Jörgensen, *Dinophysis alata* Böhm and *Dinophysis alata* (Wood) Balech is confusing. Viličić *et al.* (2002) reported *Dinophysis alata* (Wood) Balech.

[11] *Dinophysis amygdala* Balech, *Phalacroma ovum* Schütt, non *Dinophysis ovum* Schütt.

[12] This taxon resembles *Phalacroma ovatum* (Claparède *et* Lachmann) Jörgensen.

[13] *Dinophysis caudata* var. *diegensis* Kofoid.

[14] *Dinophysis intermedia* Pavillard, *Dinophysis laevis* Pouchet.

[15] *Phalacroma odiosum* Pavillard.

[16] *Phalacroma mitra* Schütt, *Phalacroma rapa* Stein, *Phalacroma dolichopterygium* Murray *et* Whitting.

[17] Non *Phalacroma ovum* Schütt.

[18] *Dinophysis infundibula* Schiller.

[19] *Dinophysis lenticula* Pavillard.

[20] *Dinophysis reticulata* (Kofoid) Balech.

[21] *Dinophysis acuminata* f. *reniformis* Pavillard, *D. pavillardii* Schröder, *D. reniformis* (Pavillard) Kofoid *et* Skogsberg, *D. ventrecta* Schiller.

[22] *Dinophysis sphaeroidea* (Schiller) Balech.

[23] *Dinophysis uracantha* Schütt, non *Dinophysis uracantha* Stein.

[24] *Dinophysis sphaerica* Pavillard

[25] A possible variety of *Histioneis depressa* Schiller (Taylor 1976, p. 44).

[26] *Ornithocercus carolinae* Kofoid, *Histiones francescae* Murray *et* Whitting.

[27] *Ornithocercus assimilis* Jörgensen, *O. galea* (Pouchet) Abé.

[28] *Histioneis splendida* Murray *et* Whitting.

[29] *Ornithocercus serratus* Kofoid, *O. orbiculatus* Kofoid *et* Michener.

[30] *Histioneis karstenii* Kofoid *et* Michener.

[31] *Dinophysis acutoides* Balech, *Phalacroma acutum* Pavillard.

[32] *Phalacroma stenopterygium* Jörgensen.

[33] *Pseudophalacroma nasutum* (Stein) Jörgensen, *Dinophysis nasuta* (Stein) Parke *et* Dixon.

[34] *Gymnodinium sanguineum* Hirasaka, *G. splendens* Lebour.

[35] *Amphidinium phaeocysticola* Lebour has been considered as a synonym of *A. crassum* Lohmann. However this synonymy is debatable (Elbrächter 1979).

[36] *Amphidinium lacustre* Stein, *A. schroederi* Schiller and *A. lacustriformis* Schiller are often considered as synonyms. Typically fresh and brackish water species.

[37] *Amphidinium klebsii* Kofoid *et* Swezy.

[38] Considered as a synonym of *Amphidinium lacustriforme* Schiller by Dodge (1982 p. 72).

[39] *Gymnodinium filum* Lebour.

[40] Taylor (1976 p. 114) reported this taxon from the Ligurian Sea.

[41] Non *Cochlodinium helix* Kofoid *et* Swezy (= *Cochlodinium helicoides* Lebour).

[42] Confusion possible between *Cochlodinium polykrikoides* Margalef (= *C. heterolobatum* Silva) and *Gymnodinium impudicum* (Fraga *et* Bravo) G. Hansen *et* Moestrup (see Cho *et al.* 2001).

[43] *Gymnodinium albulum* Lindemann and *G. simplex* (Lohmann) Kofoid *et* Swezy may be synonyms.

[44] The North European taxon, *Gyrodinium aureolum* Hulburt *sensu* Braarud *et* Heimdal, is a synonym of *Karenia mikimotoi* (Miyake *et* Kominami *ex* Oda) G. Hansen *et* Moestrup (= *Gymnodinium nagasakiense* Takayama *et* Adachi) (Hansen *et al.* 2000). See also Note 51.

[45] According to Bolch and Reynolds (2002) other taxa that also produce microreticulate cysts such as *Gymnodinium nolleri* Ellegaard *et* Moestrup and *G. microreticulatum* Bolch *et* Hallegraeff are present in the Tyrrhenian and Adriatic Seas based on the cysts reported by Montresor *et al.* (1998) and Rubino *et al.* (2000).

[46] The records of *Gymnodinium catenatum* Graham by Carrada *et al.* (1991), Giacobbe *et al.* (1995) and Labib (1997) are considered as *G. impudicum* (Fraga *et* Bravo) G. Hansen *et* Moestrup.

[47] *Gymnodinium conicum* Kofoid *et* Swezy (= *G. viridis* Lebour) is considered as a synonym of *Gyrodinium viridescens* Kofoid *et* Swezy. Non *Gyrodinium conicum* Schiller.

[48] *Gymnodinium punctatum* var. *grammaticum* Pouchet.

[49] *Gymnodinium rhomboides* Schütt, *G. hyalinum* Lebour (= *G. lucidum* Ballantine *in* Parke *et* Dixon). *Gyrodinium striatissimum* (Hulburt) G. Hansen *et* Moestrup has been considered as a synonym until the redescription of *G. heterostriatum* Kofoid *et* Swezy by Elbrächter (1994).

[50] This brackish waters taxon appears associated with *Karenia mikimotoi* (Miyake *et* Kominami *ex* Oda) G. Hansen *et* Moestrup (see also Notes 44 and 51).

[51] According to Faust and Gulledge (2002) this taxon was recorded in the Tyrrhenian Sea by Carrada *et al.* (1991). Confusion possible with species of the complex *Karenia*

mikimotoi (Miyake *et* Kominami *ex* Oda) G. Hansen *et* Moestrup. *Gymnodinium pulchellum* is distinguished from *K. mikimotoi* by the sigmoid apical groove. See also Note 44.

[52] This taxon resembles *Katodinium glaucum* (Lebour) Loeblich III.

[53] *Gyrodinium opinum* (Schütt) Lebour.

[54] *Gyrodinium dominans* Hulburt.

[55] "*lacryma*" (= tear-drop) should be the correct epithet of this taxon.

[56] *Gymnodinium spirale* var. *pepo* Schütt.

[57] *Gymnodinium spirale* var. *pinguis* Schütt.

[58] *Gymnodinium breve* Davis, *Ptychodiscus brevis* (Davis) Steidinger.

[59] Reported as *Gymnodinium galatheanum* Braarud (= *Gyrodinium galatheanum* (Braarud) Taylor *sensu* Taylor). More recently this taxon, unless *Gymnodinium galatheanum* Braarud *sensu* Kite *et* Dodge, is considered as a synonym of *Karlodinium micrum* (Leadbeater *et* Dodge) J. Larsen (Daugbjerg *et al.* 2000).

[60] *Massartia glauca* (Lebour) Schiller, *Gyrodinium glaucum* (Lebour) Kofoid *et* Swezy, *Gymnodinium minutum* Lebour, *Massartia minuta* (Lebour) Conrad *et* Kufferath, *Massartia tubulata* Rampi.

[61] *Massartia tubulata* Rampi.

[62] Related to the genus *Gyrodinium* Kofoid *et* Swezy according to Sournia (1986, p. 57).

[63] *Gymnodinium teredo* Pouchet.

[64] *Ptychodiscus inflatus* Pavillard, *P. carinatus* Kofoid.

[65] *Erythropsis agilis* Hertwig. Probably several species are reported as *E. agile* (Hertwig) P.C. Silva according to Elbrächter (1979).

[66] Elbrächter (1979) considered this taxon as a synonym of *E. agile* (Hertwig) P.C. Silva.

[67] To the best of my knowledge, never reported after the initial description by Greuet (1968b).

[68] *Pouchetia armata* Dogiel, *Pouchetia maculata* Kofoid *et* Swezy.

[69] *Kofoidinium lebourae* (Pavillard) Taylor (= *Gymnodinium lebourae* Pavillard).

[70] Originally described from the Ligurian Sea as *Leptodinium caudatum* Cachon *et* Cachon.

[71] *Pratjetella medusoides* (Hertwig) Loeblich *et* Loeblich III. Doubtful taxon (Sournia 1986, p. 53).

[72] *Abedinium dasypus* (Cachon *et* Cachon) Loeblich *et* Loeblich III.

[73] Reported from the Ligurian Sea as *Leptospathium navicula* Cachon *et* Cachon-Enjumet (1964) after the description by Margalef (1963). Balkis (2000) reported this taxon from the Marmara Sea.

[74] Resembles *Pronoctiluca acuta* (Lohmann) Schiller.

[75] *Oxytoxum margalefii* Rampi, *Oxytoxum tonollii* Rampi.

[76] *Murrayella spinosa* Kofoid, *Pavillardinium spinosum* (Kofoid) Taylor *ex* Sournia, *Amphidoma spinosa* (Kofoid) Kofoid *et* Michener, *Gonyaulax rouchii* Rampi.

[77] This taxon resembles *Ceratium incisum* (Karsten) Jörgensen.

[78] *Ceratium buceros* f. *claviger* (Kofoid) Schiller, *Ceratium horridum* f. *claviger* (Kofoid) Sournia.

[79] Also reported as *Ceratium trichoceros* var. *contrarium* (Gourret) Schiller.

[80] *Ceratium horridum* var. *lenticulatum* Jörgensen, *C. buceros* f. *denticulatum* (Jörgensen) Schiller.

[81] Reported as *Ceratium pulchellum* f. *eupulchellum* by Ghazzawi (1939) in the Canal of Suez. This taxon resembles *C. tripos* var. *pulchellum* (Schröder) López, see Sournia (1967).

[82] *Ceratium arcuatum* (Gourret) Pavillard, *C. tripos* var. *arcuatum* Gourret, non *C. arcuatum* Cleve.

[83] *Ceratium fusus* var. *extensum* Gourret.

[84] *C. tripos* var. *horridum* Cleve, but *C. tenue* (Ostenfeld *et* Schmidt) Jörgensen, *C. intermedium* (Jörgensen) Jörgensen and *C. buceros* (Zacharias) Schiller have not been considered as synonyms.

[85] This taxon resembles *Ceratium limulus* (Gourret *ex* Pouchet) Gourret.

[86] *C. tenuissimum* Kofoid.

[87] *Ceratium carriense* var. *volans* (Cleve) Sournia.

[88] *Acanthodinium caryophyllum* Kofoid.

[89] *Micracanthodinium quadrispinum* (Pavillard) Margalef.

[90] Confusion possible with *Cladopyxis brachiolata* Stein.

[91] *Heterodinium detonii* Rampi.

[92] *Crypthecodinium setense* Biecheler.

[93] *Goniodoma polyedricum* (Pouchet) Jörgensen, *Heteraulacus polyedricum* (Pouchet) Drugg *et* Loeblich, *Triadinium polyedricum* (Pouchet) Dodge, *Goniodoma polyedra* Rampi.

[94] *Heteraulacus sphaericum* (Murray *et* Whitting) Loeblich III, *Triadinium sphaericum* (Murray *et* Whittman) Dodge.

[95] Reported as *Pyrodinium schilleri* (Matzenauer) Schiller [= *Pyrodinium bahamense* Plate var. *compressum* (Böhm) Steidinger, Tester *et* Taylor].

[96] *Alexandrium lusitanicum* Balech.

[97] Reported as *Goniodoma ostenfeldii* Paulsen by Lecal (1954).

[98] Reported as *Gonyaulax subulata* Kofoid *et* Michener. This taxon resembles *Amylax triacantha* (Jörgensen) Sournia (Dodge 1982, p. 217).

[99] Reported as *Gonyaulax? triacantha* Jörgensen by Lecal (1954).

[100] *Gonyaulax spinifera* sensu Schütt.

[101] *Gonyaulax digitale* Kofoid, *Protoperidinium digitale* Pouchet.

[102] Resembles *Gonyaulax birostris* Stein.

[103] Reported by Narusevich and Tokarev (1989) in an undeterminated location of the Mediterranean Sea.

[104] The comments by Schiller (1935–1937, p. 290) on the similarity between *Gonyaulax kofoidii* and *G. pacifica* Kofoid could induce confusion between both taxa (Pavillard 1937, p. 16; Taylor 1976, p. 104).

[105] *Gonyaulax minima* Matzenauer.

[106] Resembles *Gonyaulax ovata* Matzenauer (Schiller 1935–1937, p. 289; Taylor 1976, p. 105).

[107] *Pavillardinium brianii* (Rampi) Sournia (= *Murrayella brianii* Rampi).

[108] *Gonyaulax levanderi* (Lemmermann) Paulsen, *Ceratocorys spinifera* Schröder.

[109] *Gonyaulax diacantha* (Meunier) Schiller, *Gonyaulax longispina* Lebour, *Amylax diacantha* Meunier.

[110] *Gonyaulax milneri* (Murray *et* Whitting) Kofoid, *Goniodoma milneri* Murray *et* Whitting.

[111] *Gonyaulax polyedra* Stein.

[112] *Gonyaulax grindleyi* Reinecke, non *G. reticulatum* Kofoid *et* Michener.

[113] *Heterodinium laticinctum* Kofoid.

[114] *Heterodinium pulchrum* Böhm, *Heterodinium richardii* Pavillard.

[115] *Heterodinium mediocre* f. *sinistrum* (Kofoid) Kofoid *et* Adamson.

[116] *Ostreopsis monotis* (Meunier) Lindemann.
[117] *Ceratium biconicum* Murray *et* Whitting, *Murrayella biconica* (Murray *et* Whitting) Pavillard and *Pavillardinium biconicum* Rampi are considered synonyms.
[118] *Pavillardinium intermedium* (Pavillard) de Toni (= *Murrayella intermedia* Pavillard), non *Centrodinium intermedium* Pavillard.
[119] *Pavillardinium splendidum* (Rampi) Rampi (= *Murrayella splendida* Rampi).
[120] Resembles *Corythodinium reticulatum* (Stein) Loeblich *et* Loeblich III.
[121] *Prorocentrum curvatum* Kofoid.
[122] Non *Corythodinium globosum* (Kofoid) Taylor.
[123] *Oxytoxum sceptrum* (Stein) Schröder.
[124] *Oxytoxum challengeroides* Kofoid.
[125] *Oxytoxum mediterraneum* Schiller.
[126] *Oxytoxum tenuistriatum* Rampi.
[127] This taxon resembles *Oxytoxum ovale* Schiller
[128] *Oxytoxum ligusticum* Rampi.
[129] *Oxytoxum gracile* Schiller.
[130] *Murrayella ovalis* Pavillard. See also comments on the genus by Sournia (1986, p. 73).
[131] *Gonyaulax mitra* (Schütt) Kofoid, *Oxytoxum gigas* Kofoid.
[132] Based on the germination of recent cysts (D'Onofrio *et al.* 1999).
[133] Meier *et al.* (2002) reported 14 species of calcareous dinoflagellates from recent cysts (4 new species), only this taxon that germinated from one cyst from the Levantine Basin is included.
[134] *Diplopsalis asymmetrica* (Mangin) Lindeman, *Diplopsalopsis bomba* (Stein) Dodge *et* Toriumi, *Dissodium asymmetricum* (Mangin) Loeblich III.
[135] Considered as a synonym of *Diplopelta bomba* Stein *ex* Jörgensen by Dodge (1982 p. 157).
[136] *Dissodium lenticulum* (Bergh) Loeblich III, *Glenodinium lenticula* (Bergh) Schiller.
[137] *Diplopsalis orbicularis* (Paulsen) Steidinger *et* Williams.
[138] Usually a brackish water species.
[139] *Glenodinium rotundum* (Lebour) Schiller.
[140] Originally described from the Tyrrhenian Sea as *Peridinium tyrrhenicum* Balech (Balech 1990).
[141] Nearly all of the marine species of *Peridinium* Ehrenberg have been transferred to *Protoperidinium* Bergh.
[142] *Protoperidinium quinquecorne* (Abé) Balech.
[143] This taxon presents synonyms such as *Diplopsalis minor* (Paulsen) Lindemann, *Zygabikodinium lenticulatum* (Manguin) Loeblich *et* Loeblich III, *Diplopeltopsis minor* (Paulsen) Pavillard, *Diplopsalis lenticula* f. *minor* Paulsen (see Dodge and Toriumi 1993, Elbrächter 1993).
[144] Non *Protoperidinium biconicum* (Dangeard) Balech.
[145] *Minuscula bipes* (Paulsen) Lebour.
[146] *Protoperidinium bimucronatum* (Schiller) Balech. The synonymy between *Peridinium sourniai* F.J.R. Taylor and *Protoperidinium bispinum* (Schiller) Balech is debatable.
[147] According to Schiller (1935, p. 223) *Peridinium curtipes* Jörgensen is a synonym of *Peridinium crassipes* Kofoid, consequently a confusion could be expected. *Protoperidinium crassipes* (Kofoid) Balech and *Protoperidinium curtipes* (Jörgensen) Balech are different species: 1) *Protoperidinium crassipes* (Kofoid) Balech (= *Peridinium crassipes* Kofoid), 2) *Protoperidinium curtipes* (Jörgensen) Balech (= *Peridinium crassipes* Paulsen 1907, non Paulsen 1930). See also Balech (1988, p. 110).
[148] *Peridinium decipiens* var. *curvipes* Ostenfeld, *Protoperidinium subcurvipes* (Lebour) Balech.
[149] *Protoperidinium longipes* (Karsten) Balech.
[150] According to Balech (1976) this taxon is related to the freshwater species *Protoperidinium achromaticum* (Levander) Balech.
[151] *Protoperidinium ovatum* Pouchet [= *P. globulus* var. *ovatum* (Pouchet) Schiller, *Peridinium ovatum* (Pouchet) Schütt] have been considered as synonyms.
[152] This taxon can be confused with *Protoperidinium ovum* (Schiller) Balech.
[153] Also reported from the Tyrrhenian Sea based on cysts by Montresor *et al.* (1998).
[154] *Protoperidinium spiniferum* (Schiller) Balech.
[155] The orthographic similarity between *P. sphaeroides* (Dangeard) Balech and *P. sphaeroideum* (Mangin) Balech is confusing (Sournia 1978, p. 29).
[156] This taxon resembles *Protoperidinium brachypus* (Schiller) Balech.
[157] *Protoperidinium angustum* (Dangeard) Balech.
[158] Most of the recently described species of *Scrippsiella* Balech *ex* Loeblich are reported from the germination of cysts (Montresor *et al.* 1994, D'Onofrio *et al.* 1999).
[159] *Scrippsiella faeroense* Dickensheets *et* Cox, non *Scrippsiella faeroense* (Paulsen) Balech *et* Soares.
[160] Reported by Rampi (1941) as *Blepharocysta striata* Schütt (see Carbonell-Moore 1994).
[161] *Podolampas spinifer* Pavillard.
[162] *Tuberculodinium vancampoae* (Rossignol) Wall (= *Pterospermopsis vancampoae* Rossignol). Taylor (1976 p. 183) reported the presence of this taxon in the Mediterranean Sea based on Margalef (1948).
[163] One specimen that resembles *C. yeye* Margalef from the Alborán Sea, one specimen of *C. yeye* and other undeterminated species of this genus were observed from the Balearic coasts (unpublished obs.). *Ceratoperidinium mediterraneum* Abboud-Abi Saab requires a more detailed description.
[164] Iwataki *et al.* (2002) reported this taxon based on the material from the Aegean Sea by Pennik and Clarke (1977).
[165] *Cachonina niei* Loeblich III.
[166] *Katodinium rotundatum* (Lohmann) Loeblich III, *Massartia rotundata* (Lohmann) Schiller, *Amphidinium rotundatum* Lohmann, *Katodinium minutum* (Lebour) Sournia.
[167] *Cladopyxis bacillifera* Schiller.
[168] *Cladopyxis claytonii* Holmes.
[169] *Cladopyxis setifera* Lohmann, *Micracanthodinium bacilliferum* (Schiller) Deflandre.
[170] The genus *Exuviella* was included in *Prorocentrum* by Dodge (1975). McLachlan *et al.* (1997) proposed the separation of both genera.
[171] Schiller (1931–1933, p. 26) reported this taxon as *Exuviella* (?) *aperta* Schiller (described from the Adriatic Sea in 1928). Inadequate description according to Dodge (1975).
[172] *P. micans* var. *gibbosum* Schiller, *P. gibbosum* (Schiller) Schiller, *P. blatta* Athanassopoulos. Resembles *Prorocentrum micans* Ehrenberg.
[173] According to Dodge (1975): *Prorocentrum bidens* Schiller, *P. lebourae* Schiller, *Exuviella oblonga* Schiller [= *Prorocentrum oblongum* (Schiller) Taylor], *E. lenticulata* Matzenauer, *E. elongata* Rampi.
[174] *Prorocentrum pyriformis* (Schiller) Hasle.

[175] *Prorocentrum minimum* (Pavillard) Schiller and *Prorocentrum cordatum* (Ostenfeld) Dodge may be synonyms (Velikova and Larsen 1999).

[176] *Prorocentrum obtusidens* Schiller, also *P. monacense* Kufferath described in the Ligurian Sea (Kufferath 1957).

[177] *P. hentschelii* Schiller, *P. sigmoides* Böhm, *P. macrurus* Athanassopoulos. Resembles *P. micans* Ehrenberg.

[178] According to Dodge (1975): *Prorocentrum mexicanum* Osorio-Tafall, *P. obtusum* Ostenfeld, *P. brochi* Schiller, *P. ovale* Schiller, *P. ovalis* Rampi, *P. rampii* Sournia.

[179] *Prorocentrum schilleri* Böhm *in* Schiller.

[180] *Prorocentrum nanum* Schiller and *P. pusillum* (Schiller) Loeblich were considered as synonyms until Puigserver and Zingone (2002).

[181] *Prorocentrum cornutum* Schiller.

[182] *Prorocentrum sphaeroideum* Schiller. *P. robustum* Osorio Tafall.

[183] *Prorocentrum adriaticum* Schiller.

[184] This taxon resembles *Prorocentrum mexicanum* Osorio-Tafall that is here considered a synonym of *Prorocentrum maximum* (Gourret) Schiller.

[185] Regarded as a doubtful dinoflagellate by Sournia (1986, p. 37).

[186] *Dissodinium* is a genus of parasitic dinoflagellates with a complicate life cycle including planktonic life cycle stages similar to those of the genus *Pyrocystis*. In contrast, *Pyrocystis* is a permanently free-living phototrophic dinoflagellate with a predominant coccoid stage and a flagellated dinospore stage (e.g., Elbrächter *et al.* 1987).

[187] *Pyrocystis lunula* (Schütt) Schütt, *Dissodinum lunula* (Schütt) Pascher.

[188] *Dissodinium fusiformis* (Thompson *ex* Murray) Matzenauer.

[189] *Dissodinium gerbaultii* (Pavillard) F.J.R. Taylor

[190] Léger (1973) reported the presence of this taxon in the Spanish Mediterranean coast by Margalef *et al.* (1957). Drebes (1981) reported that *Pyrocystis margalefii* Léger is probably identical with the resting stages of *Dissodinium pseudolunula* Swift *ex* Elbrächter *et* Drebes.

[191] *Dissodinium minimum* Matzenauer.

[192] *Pyrocystis pseudonoctiluca* Wyville-Thomson *ex* Murray, *Dissodinium pseudolunula* Swift *ex* Elbrächter *et* Drebes.

[193] Regarded as a doubful dinoflagellate by Sournia (1986, p. 97). Commonly reported as *Adinomonas* Schiller.

[194] Regarded as a doubtful dinoflagellate by Sournia (1986, p. 97).

[195] Doubtful taxon (Sournia 1986, p. 98). Also reported from the Sicilian coasts or North-Italian lakes by Andreis *et al.* (1982).

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An annotated checklist of dinoflagellates in the Black Sea

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Abstract

An annotated checklist of free-living dinoflagellates (Dinophyceae) of the Black Sea, based on literature records, is reported and compared to the Mediterranean Sea and world oceans. Toxic species and/or responsible of harmful algal blooms (HAB) are marked in the checklist. From the 267 species (54 genera) listed nearly all taxa can be considered as cosmopolitan and no species as endemic. Several typically Arctic-boreal species (non recorded from the Mediterranean Sea) are reported from the Black Sea. The taxonomy and the biogeography of the taxa are discussed.

Introduction

The Black Sea (~41–46° N) is a semi-enclosed basin whose only connection to the world's oceans is through narrow straits (<110 m depth), the Dardanelles and the Bosphorus, both opening to the Marmara Sea. The fresher waters of the Black Sea (salinity ~17) flow to the Mediterranean Sea by means of an upper layer flow; saltier Mediterranean waters (~38.5) flow to the Black Sea in a lower current. A permanent halocline is maintained by colder low-salinity surface water averaging 17.5–19 overlying deep waters with salinity about 22. Low near-surface salinity is maintained by the influx of freshwater from rivers and decreases to <13 near the mouths of the Danube and Dnieper rivers (see references in Sorokin, 2002).

In the last decades the Black Sea basin has experienced huge changes in water quality caused by human interventions both on the hydraulic regime of the rivers and on the nutrient and pollutant discharge. Significant changes on phytoplankton, zooplankton, zoobenthos and fisheries have been reported (Bakan & Buyukgungor, 2000). The high nitrate and phosphate to silicate ratios as well as organic material provide competitive advantage for mixo- or heterotrophic dinoflagellates compared to autotrophic diatoms, with high dinoflagellates to diatoms ratio (Humborg et al., 1997). A change in dominant species was observed as well as an increase in red tide events (Bologa et al., 1995; Mihnea, 1997). The high degree of eutrophication in the Black Sea could favour invasive species (i.e., via ballast waters; Moncheva & Kamburska, 2002) to compete for niches. Among phytoplankton taxa, dinoflagellates with more than 200 potential toxic species (Sournia, 1995) require special attention.

Krakhmalny (1994) reported a list of 193 dinoflagellates (including infraespecific taxa) in the Black Sea. Other checklists are available from Georgian (Komakhidze & Mazmanidi, 1998), Ukrainian (Zaitsev & Alexandrov, 1998), Turkish (Ozturk, 1999; Turkoglu & Koray, 2000, 2002; Koray et al., 2000), Bulgarian (Konsulov, 1998; Velikova et al., 1999) and Romanian coasts (Skolka, 1977; Bodeanu, 1987–1988; Petranu, 1997).

Literature sources are compiled here and an annotated checklist is discussed. This study attempts to assess the biodiversity of dinoflagellates, here defined

as species richness, in the Black Sea and also to compare this richness to adjacent seas in order to establish the biogeographical affinities of the Black Sea dinoflagellates.

Material and methods

This study is based on literature records of dinoflagellates from the Black Sea (108 references). The species are arranged alphabetically and taxa are named with their nomenclatural authorities (Table 1). The nomenclature is updated and the synonyms are reported. The numbers following a species name in the checklist refer to the list of references. Exclusively freshwater taxa such as *Ceratium hirundinella* (O.F. Müller) Bergh, parasitic species such as *Paulsenella chaetoceratis* (Paulsen) Chatton or taxa insufficiently known or of doubtful validity such as the genera *Cystodinium* Klebs or *Hypnodinium* Klebs have been excluded. However the primarily freshwater species (see Popovský & Pfiester, 1990) that apparently are able to tolerate the salinity of the offshore waters of the Black Sea are listed, although not considered for biogeographical purposes.

The species included in what are considered to be valid or reliable records are reported in bold type. The records of insufficiently known or dubious species, requiring more precise taxonomical investigation, are presented in normal type. Most of these taxa mainly correspond to athecate dinoflagellates. It should be taken into account that the fixatives commonly used (Lugol, formaldehyde) do not sufficiently preserve them to allow species identification. Body shape and morphology often change during the process of fixation so that it is even difficult to determine the genus. In addition, some of the older descriptions are not sufficiently detailed or are inappropriate – as also occurred for some thecate species [i.e., *Protoperidinium sinaicum* (Matzenauer) Balech, *P. deficiens* (Meunier) Balech].

The taxa considered as Harmful Algal Bloom (HAB) species are based on the species listed by Faust & Gulledge (2002) and Hallegraeff (2002) as well as *Amphidinium operculatum* Claparède *et* Lachmann and *Heterocapsa triquetra* (Ehrenberg) Stein.

The Black Sea taxa have been compared to those in checklists from the Mediterranean and the adjacent seas. References concerning the presence of the taxa in the Mediterranean Sea are omitted due to space limitation, but can be found in Gómez (2003). Literary resources from other geographical areas are cited in the text where appropriate.

Results and discussion

The Black Sea dinoflagellates flora is represented by 267 species from 54 genera (Table 1), being about one half monotypic genera (30 genera). The most numerous genera were *Protoperidinium* Bergh *emend.* Balech (41 species), *Ceratium* Schrank (26 species) and *Dinophysis* Ehrenberg (20 species) as well as the primarily freshwater genera *Glenodinium* (Ehrenberg) Stein, *Peridinium* Ehrenberg (also *Glenodiniopsis* Woloszynska, *Peridiniopsis* Lemmermann) and species of *Gymnodinium* Stein (30 species) that are able to tolerate a wide range of salinity.

Concerning the geographical distribution, nearly all the Black Sea species can be considered as cosmopolitan with some exceptions as discussed below.

Species richness and biodiversity

About 1400–1800 species (115–131 genera) constitute marine living dinoflagellates in the world oceans (Sournia, 1995; Steidinger & Tangen, 1997). According to this non-updated value, the Black Sea comprises about 15% of the world species and about 40% of the dinoflagellate genera (54 genera).

This low species richness compared to the Mediterranean Sea (673 species, 104 genera; Gómez, 2003) is primarily attributable to the general low diversity in brackish waters, usually more stressed than marine waters. The low transparency and the toxic deep layer (most of the deeper waters are isolated from any source of oxygen, and have a high content of hydrogen sulphide) reduce the biotic layer. Consequently the oxygenic life is restricted to the upper waters, decreasing the number of niches available compared to oceanic waters [for example for the deep-living flora (Sournia, 1982)]. The contents of organic matter could favour a high species richness of heterotrophic dinoflagellates as Noctilucales and partially Gymnodiniales, the latter usually difficult to identify at species level. Stoyanova (1999) reported high abundance (85–170 cells l^{-1}) of the aberrant heterotrophic dinoflagellates *Spatulodinium pseudonoctiluca* (Pouchet) Cachon *et* Cachon *ex* Loeblich *et* Loeblich III, *Scaphodinium mirabile* Margalef and *Petalodinium porcelio* Cachon *et* Cachon. She suggested that the high abundance of these new records in the Black Sea is a consequence

Table 1. List of taxa. The species considered as valid records are reported in bold type. The records of insufficiently known, questionable or dubious species, requiring more precise taxonomical investigation, are presented in normal type. The numbers following a species name in the checklist refer to the list of references. HAB = Harmful Algal Bloom species; Cold = typical species from cold waters; Pacif. = apparently Indo-Pacific species.

	Achradina pulchra Lohmann [128]
HAB	***Akashiwo sanguinea*** (Hirasaka) G. Hansen *et* Moestrup [= *Gymnodinium sanguineum* Hirasaka, *G. splendens* Lebour, *G. nelsonii* Martin] [9,12,15,17–20,23,27,33,34,37,59,61,75,78,89,94,96,110,114,117,119,127,133–135,143]
HAB	*Alexandrium monilatum* (Howell) Balech [= *Gonyaulax monilata* Howell, *Gessnerium mochimaensis* Halim *ex* Halim, *G. monilata* (Howell) Loeblich, *Pyrodinium monilatum* (Howell) F.J.R. Taylor] [23,59,75,76,78,79,137,139]
HAB, cold	***Alexandrium ostenfeldii*** (Paulsen) Balech *et* Tangen [= *Goniodoma ostenfeldii* Paulsen, *Gonyaulax ostenfeldii* (Paulsen) Paulsen, *Protogonyaulax ostenfeldii* (Paulsen) Fraga *et* Sánchez, *Heteraulacus ostenfeldii* (Paulsen) Loeblich, *Gessnerium ostenfeldii* (Paulsen) Loeblich *et* Loeblich III, *Triadinium ostenfeldii* (Paulsen) Dodge] [61,96]
	Amphidinium acutissimum Schiller [= *A. acutum* Schiller, non *A. acutum* Lohmann] [132]
	Amphidinium amphidinioides (Geitler) Schiller [= *A. geitleri* Huber-Pestalozzi, *A. wigrense* Woloszynska, *A. bourrellyi* Wawrik, *Gymnodinium amphidinioides* Geitler] [61,132]
	Amphidinium conradii Schiller [= *Gymnodinium glaucum* Conrad] [61]
	Amphidinium crassum Lohmann [= *A. phaeocysticola* Lebour] [59,61,143]
Pacif.	*Amphidinium cucurbita* Kofoid *et* Swezy [61]
	Amphidinium curvatum Schiller [61]
	Amphidinium elenkinii Skvortsov [= *A. larvale* Lindemann, *A. hyalinum* Entz, *A. tatrae* Woloszynska, *A. tenagodes* Harris, *A. luteum* Skuja, *A. gyrinum* Harris, *A. turicense* Huber-Pestalozzi, *A. lohamari* Skuja, *A. skujae* Christen, *Gymnodinium rarum* Litvinenko] [132]
Cold	*Amphidinium extensum* Wulff [61,96,110,114,119]
	Amphidinium flagellans Schiller [61]
	Amphidinium globosum Schröder [61]
	Amphidinium lacustre Stein [= *A. lacustriforme* Schiller, *A. schroederi* Schiller] [132]
	Amphidinium lanceolatum Schröder [58,132]
Cold	*Amphidinium longum* Lohmann [= *A. acutum* Lohmann, non *A. acutum* Schiller] [59,61]
HAB	***Amphidinium operculatum*** Claparède *et* Lachmann [= *A. klebsii* Kofoid *et* Swezy, *A. massartii* Biecheler, *A. wislouchii* Hulburt, *A. hoefleri* Schiller *et* Diskus] [59,61]
	Amphidinium ovum Herdman [58,61]
	Amphisolenia bidentata Schröder [non *A. bidentata* Pavillard, non *A. bidentata* Okamura] [94]
Cold	*Amylax triacantha* (Jørgensen) Sournia [= *Gonyaulax triacantha* Jørgensen, *Amylax lata* Meunier] [61]
	Centrodinium intermedium Pavillard [1]
	Ceratium belone Cleve [= *C. pacificum* Schröder] [60,133,134]
	Ceratium buceros (Zacharias) Schiller [94]
	Ceratium candelabrum (Ehrenberg) Stein [8,61,94]
	Ceratium carriense Gourret [= *C. volans* Pavillard, *C. massiliense* Pavillard] [60,133,134]
	Ceratium compressum Gran [for synonymy with *C. platycorne*, see Balech (1988: 141)] [60,133,134]
	Ceratium declinatum (Karsten) Jørgensen [= *C. tripos declinatum* Karsten] [60,133,134]
	Ceratium extensum (Gourret) Cleve [= *C. strictum* (Okamura *et* Nishikawa) Kofoid, *C. biceps* Kofoid] [8,9,18,60,61,94,96,133,134]
	Ceratium falcatum (Kofoid) Jørgensen [= *C. pennatum* f. *falcata* Kofoid, *C. pennatum* var. *falcatum* Jørgensen] [61,94]
	Ceratium furca (Ehrenberg) Claparède *et* Lachmann [= *C. bipes* Claparède *et* Lachmann] [8,9,14,15,18–20, 33,34,46,59–61,74–76,79,90,94,96,107,109–111,114,119,125,132–135,143]
	Ceratium fusus (Ehrenberg) Dujardin [var. *fusus*, var. *seta* and var. *schuettii*] [2,8,9,18,27,33–35, 42,46,59–61,74,79,85,90,94,96,99,107,109,110–112,114,119,125,133–135,143,144]
	Ceratium hexacanthum Gourret [= *C. reticulatum* (Pouchet) Cleve] [60,61,94,133,134]
	Ceratium horridum (Cleve) Gran [= *C. tripos* var. *horridum* Cleve, *C. intermedium* (Jørgensen) Jørgensen, *C. claviger* Kofoid, *C. tenue* (Ostenfeldet Schmidt) Jørgensen, *C. inclinatum* Kofoid, *C. tenuissimum* Kofoid, *C. mollis* Kofoid, *C. batavum* Paulsen, *C. leptosomum* Jørgensen, *C. horridum* var. *denticulatum* Jørgensen] [60,94,133–135]
	Ceratium incisum (Karsten) Jørgensen [60,133,134]
	Ceratium inflatum (Kofoid) Jørgensen [8,60,61,94,114,133–135,
	Ceratium kofoidii Jørgensen [60,133,134]
	Ceratium lineatum (Ehrenberg) Cleve [60,61,133,134]

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Table 1. Continued.

Cold	***Ceratium longipes*** (Bailey) Gran [= *C. arcticum* var. *longipes* (Bailey) Graham *et* Bronikovsky] [61,94]
	Ceratium longirostrum Gourret [60,94,132–135]
	Ceratium macroceros (Ehrenberg) Cleve [8,61,94,114]
	Ceratium massiliense (Gourret) Karsten [also var. *armatum* (Karsten) Jørgensen] [60,61,133,134]
	Ceratium minutum Jørgensen [59,61]
	Ceratium pentagonum Gourret [46,61,94,135,]
	Ceratium pulchellum Schröder [= *C. tripos* var. *pulchellum* Peters] [60,94,133,134]
	Ceratium teres Kofoid [61,133,134]
	Ceratium tripos (O.F. Müller) Nitzsch [= *C. schroederi* Nie, *C. neglectum* Ostenfeld, *C. tripodioides* (Jørgensen) Steemann Nielsen] [8,9,18,31,33,34,42,46,58,60,61,74,79,90,94,96,99,107,109,110,114,119,125,133–135]
	Ceratium volans Cleve [= *C. carriense* var. *volans* (Cleve) Sournia, non *C. volans* Pavillard] [60,133,134]
	Cladopyxis brachiolata Stein [= *C. spinosa* (Kofoid) Schiller] [61]
	Cochlodinium adriaticum Schiller [= *Gyrodinium adriaticum* Schiller] [61,86,88]
	Cochlodinium brandtii Wulff [144]
	Cochlodinium citron Kofoid *et* Swezy [61,128,144]
	Cochlodinium geminatum (Schütt) Schütt [= *Gymnodinium geminatum* Schütt] [132]
	Cochlodinium helicoides Lebour [= *C. helix* Schütt pro parte, *C. helix* Kofoid *et* Swezy, reported as synonym *C. helix* (Pouchet) Lemmermann] [61,128]
	Cochlodinium lebourae Kofoid *et* Swezy [61]
	Cochlodinium pirum (Schütt) Lemmermann [= *Gymnodinium pirum* Schütt] [61]
	Corythodinium compressum (Kofoid) F.J.R. Taylor [= *Oxytoxum compressum* Kofoid] [133]
	Corythodinium diploconus (Stein) F.J.R. Taylor [= *Oxytoxum diploconus* Stein] [133]
HAB	***Dinophysis acuminata*** Claparède *et* Lachmann [= *D. ovum* var. *baltica* Paulsen, *D. arctica* sensu Woloszynska, *D. baltica* (Paulsen) Woloszynska, *D. cassubica* Woloszynska, *D. levanderi* Woloszynska, *D. paulsenii* Woloszynska, *D. boehmii* Paulsen, *D. borealis* Paulsen, *D. lachmannii* Paulsen, *D. skagii* Paulsen] [9,18,59–61,94,96,114,133–135,143]
HAB	***Dinophysis acuta*** Ehrenberg [= *D. dens* Pavillard, *D. groenlandica* (Schiller) Balech] [46,59–61,89,94,133,134]
Cold	*Dinophysis apiculata* Meunier [61]
Cold	*Dinophysis arctica* Mereschkowsky [= *D. laevis* (Bergh) Pouchet, *D. rotundata* Levander, *D. granulata* Cleve, non *D. laevis* Bergh, non *D. rotundata* Claparède *et* Lachmann, non *D. arctica* sensu Woloszynska] [61]
HAB	***Dinophysis caudata*** Saville-Kent [= *D. homunculus* Stein, *D. diegensis* Kofoid] [9,18,34,46,59–61,90,94,96,108,114,119,133–135,143]
	Dinophysis dentata Schiller [94]
HAB	***Dinophysis fortii*** Pavillard [= *D. laevis* Pouchet, *D. lapidistrigiliformis* Abé, *D. intermedia* Pavillard] [33,46,61,94,110,114,125,133–135,143]
HAB	***Dinophysis hastata*** Stein [non *Phalacroma hastatum* Pavillard, non *Ph. hastatum* Hensen] [9,18,34,59–61,94,96,110,114,133,134]
	Dinophysis meunieri Schiller [= *D. cuneiformis* Meunier, non *D. cuneiformis* Mangin] [34]
	Dinophysis minuta (Cleve) Balech [= *Phalacroma minutum* Cleve] [61]
HAB, cold	*Dinophysis norvegica* Claparède *et* Lachmann [= *D. debilior* (Paulsen) Paulsen, resembles to *D. acuta* Ehrenberg] [61,143]
	Dinophysis ovum Schütt [= *D. brevisulcus* Tai *et* Skogsberg pro parte, non *Phalacroma ovum* Schütt] [1,9,18,58,59,61,94,96,110,114,135,143]
	Dinophysis parva Schiller [= *D. infundibula* Schiller] [60,94,133,134]
	Dinophysis punctata Jørgensen [non *D. punctata* Balech] [60,94,133,134]
HAB	***Dinophysis sacculus*** Stein [= *D. acuminata* f. *reniformis* Pavillard, *D. reniformis* (Pavillard) Kofoid *et* Skogsberg, *D. pavillardii* Schröder, *D. ventrecta* Schiller, *D. phaseolus* Silva] [9,15,17–20,33,34,59–61,90,94,96,107–110,114,119,133–135,143]
	Dinophysis schilleri Sournia [= *Phalacroma sphaeroideum* Schiller] [59,61,96]
	Dinophysis schuettii Murray *et* Whitting [= *D. uracantha* Schütt, non *D. uracantha* Stein] [61]
	Dinophysis similis Kofoid *et* Skogsberg [= *D. sphaerica* Schütt, *D. simplex* Balech, *D. tai* Balech, non *D. simplex* Böhm] [94]
	Dinophysis sphaerica Stein [= *D. vanhoffenii* Ostenfeld] [61,94,96,143]
HAB	***Dinophysis tripos*** Gourret [= *D. caudata* var. *tripos* (Gourret) Gail] [61]
	Diplopelta bomba Stein *ex* Jørgensen [= *Diplosalis lenticula* Stein, *Peridiniopsis asymmetrica* Mangin, *Diplopelta asymmetrica* (Mangin) Lebour, *Diplopsalopsis asymmetricum* (Mangin) Abé, *Dissodium asymmetricum* (Mangin) Loeblich III] [94]

Continued on p. 47

Table 1. Continued.

Diplopsalis lenticula Bergh [= *Glenodinium lenticula* (Bergh) Schiller, *Dissodium lenticulum* (Bergh) Loeblich III] [8,9,18,33,34,59–61,85,88,89,96,109–112,114,119,128,133,134,143]

Diplopsalopsis orbicularis (Paulsen) Meunier [= *Peridinium orbiculare* Paulsen] [9,18,61,96,114,128,143]

Glenodinium behningii (Lindemann) Kisselew [= *Diplopsalis behningii* Lindemann] [61,114,143]

Glenodinium caspicum (Ostenfeld) Schiller [61,110,143]

Glenodinium inflatum Meunier [18,61,96]

Glenodinium obliquum Pouchet [61]

Glenodinium paululum Lindemann [9,15,18–20,27,34,42,59,61,88,89,96,107,109,110,114,117,119,143]

Glenodinium pilula (Ostenfeld) Schiller [= *Diplopsalis pilula* Ostenfeld, *Peridinium pilula* (Ostenfeld) Lemmermann] [9,14,15,18–20,34,58,59,61,96,114,143]

Glenodinium pulvisculus (Ehrenberg) Stein [= *Peridinium pulvisculus* Ehrenberg] [61]

Goniodoma acuminatum (Ehrenberg) Stein [= *Peridinium acuminatum* Ehrenberg, non *Peridinium polyedricum* Pouchet] [61,94]

Goniodoma polyedricum (Pouchet) Jørgensen [= *Peridinium polyedricum* Pouchet, *Triadinium polyedricum* (Pouchet) Dodge, *Goniodoma acuminata* Stein pro parte, non *Peridinium acuminatum* Ehrenberg] [9,18,59,61,96,110,143]

Gonyaulax africana Schiller [94,135]

Gonyaulax apiculata (Pénard) Entz [= *G. apiculata* var. *clevei* Ostenfeld, *Peridinium apiculatum* Pénard, *G. clevei* Ostenfeld, *G. polonica* Woloszynska, *G. limmetica* Lindemann, *G. austriaca* Schiller] [8,33,34,59]

Gonyaulax birostris Stein [= *Gonyaulax glyptorhynchus* Murray *et* Whitting, *G. highleyi* Murray *et* Whitting] [60,133,134]

Cold ***Gonyaulax cochlea*** Meunier [= *G. polygramma* Meunier] [9,18,22,25,58,59,61,94,96,114,117]

Gonyaulax diegensis Kofoid [= *G. spinifera* sensu Schütt] [9,18,34,46,59–61,94,96,114,119,133,134,143]

Gonyaulax digitalis (Pouchet) Kofoid [= *G. spinifera* Stein, *Protoperidinium digitale* Pouchet] [8,18,59,61,94,96,114,119]

Gonyaulax elegans Rampi [94,135]

Gonyaulax fragilis (Schütt) Kofoid [= *Steiniella fragilis* Schütt] [61]

Gonyaulax gracilis Schiller [61]

Gonyaulax minuta Kofoid *et* Michener [= *G. minima* Matzenauer] [58,59,61,89,131]

Gonyaulax monacantha Pavillard [60,94,133,134]

Gonyaulax monospina Rampi [94]

Gonyaulax orientalis Lindemann [= *Goniodoma orientale* (Lindemann) Balech, *Triadinium orientale* (Lindemann) Dodge, *Gonyaulax lebourae* Balech pro parte, non *G. orientalis* sensu Lebour] [59,61]

HAB ***Gonyaulax polygramma*** Stein [= *G. schuettii* Lemmermann] [8–15,17,18,25–28,34,59–61,68,69,72,73,94,96,110,114,115,119,133,134,137,143]

Gonyaulax scrippsae Kofoid [58,59,61,143]

Gonyaulax spinifera (Claparède *et* Lachmann) Diesing [=*G. levanderi* (Lemmermann) Paulsen, non *G. spinifera* Stein] [8,9,18,46,59–61,89,94,96,109,114,131,133,134]

Gonyaulax verior Sournia [= *G. diacantha* (Meunier) Schiller, *G. longispina* Lebour, *Amylax diacantha* Meunier] [46]

Gymnodinium agile Kofoid *et* Swezy [non *G. agile* sensu Herdmann] [9,18,59,61,96,110,114,117]

Gymnodinium agiliforme Schiller [58,61,89,96]

Gymnodinium aeruginosum Stein [= *G. acidotum* Nygaard, *G. viride* Pénard, *G. campaniforme* Popovský] [132]

Gymnodinium auratum Kofoid *et* Swezy [119]

Gymnodinium biconicum Schiller [1,94]

Gymnodinium conicum Kofoid *et* Swezy [= *G. viridis* Lebour] [59]

Gymnodinium flavum Kofoid *et* Swezy [non *Gyrodinium flavum* Kofoid] [59]

Gymnodinium fuscum (Ehrenberg) Stein [= *G. caudatum* Prescot, *Cystodinium gessneri* (Baumeister) Bourrelly] [9,18,96,119]

Gymnodinium gracile Bergh [= *G. spirale* var. *nobilis* Pouchet, *G. roseum* Lohmann, *G. abbreviatum* Kofoid *et* Swezy, *G. lohmannii* Paulsen] [128]

Gymnodinium helveticum Pénard [= *G. helveticum* var. *apiculata* (Zacharias) Utermöhl, *Glenodinium apiculatum* Zacharias *in* Schilling] [12,15,17,19,20,27,59,61,96,119,143]

Gymnodinium galeaeforme Matzenauer [59]

Gymnodinium gibbera Schiller [119]

Gymnodinium grammaticum (Pouchet) Kofoid *et* Swezy [= *G. punctatum* var. *grammaticum* Pouchet] [61]

Gymnodinium lachmannii Saville-Kent [59]

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Table 1. Continued.

Gymnodinium marinum Saville-Kent [61]

Gymnodinium minus Lebour [61]

Gymnodinium najadeum Schiller [19–22,25,34,58,59,61,75,76,79,89,96,119,143]

Gymnodinium neapolitanum Schiller [61,96,114,143]

Gymnodinium paradoxum Schilling [27,96]

Gymnodinium pygmaeum Lebour [possibly identical with *Gymnodinium aureolum* (Hulburt) G. Hansen] [61]

Pacif. *Gymnodinium radiatum* Kofoid *et* Swezy [62]

Gymnodinium rhomboides Schütt [9,12,14,15,17–20,33,34,58,59,61,90,96,110–112,114,119]

Gymnodinium rotundatum Klebs [94]

Gymnodinium semidivisum Schiller [61]

Gymnodinium simplex (Lohmann) Kofoid *et* Swezy [= *Protodinium simplex* Lohmann] [1,61,94]

Gymnodinium sphaericum (Calkins) Kofoid *et* Swezy [= *G. gracile* var. *sphaerica* Calkins] [117]

Pacif. *Gymnodinium sulcatum* Kofoid *et* Swezy [61,143]

Gymnodinium uberrimum (Allman) Kofoid *et* Swezy [= *G. mirabile* Pénard, *G. mirabile* var. *rufescens* Pénard, *G. rufescens* Lemmermann, *G. bogoriense* Klebs, *G. rotundatum* Klebs, *G. obesum* Schiller, *G. limneticum* Woloszynska, *G. poculiferum* Skuja, *G. limitatium* Skuja, *G. irregulare* Christen, *G. uberrimum* var. *rotundatum* Popovský, *Gyrodinium traunsteineri* Lindemann, *Melodinium uberrimum* Kent, *Peridinium uberrima* Allman] [23,75,76,132,139]

Gymnodinium variabile Herdman [61]

Cold *Gymnodinium wulffii* Schiller [non *Gyrodinium wulffii* Schiller] [58,59,61]

Cold *Gyrodinium britannicum* Kofoid *et* Swezy [= *Spirodinium spirale* var. *acutum* Lebour] [61]

Gyrodinium capsulatum Kofoid *et* Swezy [61]

Gyrodinium cornutum (Pouchet) Kofoid *et* Swezy [= *Gymnodinium spirale* var. *cornutum* Pouchet] [85,86,132]

Gyrodinium dorsum Kofoid *et* Swezy [61]

Gyrodinium falcatum Kofoid *et* Swezy [= *Gymnodinium fusus* Schütt pro parte, *Pseliodinium vaubanii* Sournia] [9,14,15,18–20,34,61,96,110,119,143]

Gyrodinium fissum (Levander) Kofoid *et* Swezy [= ?*G. fissoides* Elbrächter, ?*Gymnodinium fissum* Levander] [59,61,144]

Gyrodinium fusus (Meunier) Akselman [= *Spirodinium fusus* Meunier, *G. fusiforme* Kofoid *et* Swezy] [9,18,26,27,29,33,34,42,59,61,79,94,96,107,114,117,119,128,143]

Gyrodinium glaebum Hulburt [= *Gymnodinium mirabile* Pénard] [61]

Gyrodinium lachryma (Meunier) Kofoid *et* Swezy [= *Spirodinium lachryma* Meunier] [9,18,27,33,34,59,61,94,96,114,117,119,128,135,143]

Gyrodinium nasutum (Wulff) Schiller [= *Spirodinium nasutum* Wulff] [59,61,96,117,128,143]

Gyrodinium pavillardii Biecheler [96]

Gyrodinium pellucidum (Wulff) Schiller [= *Gymnodinium pellucidum* Wulff] [94]

Gyrodinium pingue (Schütt) Kofoid *et* Swezy [= *Gymnodinium spirale* var. *pinguis* Schütt, *Spirodinium varians* Wulff] [9,18,59,61,96,112,114,143]

Gyrodinium prunus (Wulff) Lebour [= *Spirodinium prunus* Wulff] [61]

Gyrodinium pusillum (Schilling) Kofoid *et* Swezy [= *Spirodinium pusillum* (Schilling) Lemmermann, *Gymnodinium pusillum* Schilling] [94]

Gyrodinium spirale (Bergh) Kofoid *et* Swezy [= *Gymnodinium spirale* Bergh] [59,61,128]

Heterocapsa rotundata (Lohmann) G. Hansen [= *Amphidinium rotundatum* Lohmann, *A. pellucidum* Redeke, *Gymnodinium minutum* Lebour, *Katodinium rotundatum* (Lohmann) Fott, *K. minutum* (Lebour) Sournia, *Massartia rotundata* (Lohmann) Schiller] [61]

HAB ***Heterocapsa triquetra*** (Ehrenberg) Stein [= *Glenodinium triquetrum* Ehrenberg, *Peridinium triquetrum* (Ehrenberg) Lebour, *Properidinium heterocapsa* (Stein) Meunier] [9,18–23,25,27,28,34,41,58–61,70,75,76,78,85,86,88,89,94,96,97,110,132–135,137,139,143]

Heterodinium murrayi Kofoid [94]

~~***Katodinium fungiforme***~~ (

Schiller, *M. austriacum* Schiller, *Katodinium crassifilum* (Schiller) Loeblich III, *K. austriacum* (Schiller) Loeblich III] [59,132]

Katodinium vorticella (Stein) Loeblich III [= *Gymnodinium vorticella* Stein, *Peridinium vorticella* Stein, *Massartia vorticella* (Stein) Schiller, *M. pratensis* Baumeister, *Katodinium viride* Christen, *K. vernale* Christen, *K. pratensis* (Baumeister) Loeblich III] [59,61]

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Table 1. Continued.

Kolkwitziella acuta (Apstein) Elbrächter [= *Glenodinium acutum* Apstein, *Diplopsalis acuta* (Apstein) Entz, *Entzia acuta* (Apstein) Lebour, *Peridinium latum* Paulsen, *Kolkwitziella salebrosa* Lindemann, *K. gibbera* (Lindemann) Lindemann, *Apsteinia acuta* Abé] [61,96,119,143]

HAB ***Kryptoperidinium foliaceum*** (Stein) Lindemann [= *Glenodinium foliaceum* Stein] [18,59,61]

HAB ***Lingulodinium polyedra*** (Stein) Dodge [= *Gonyaulax polyedra* Stein] [8,9,14,15,17–20,23,25,33,46,58–61,72,75,76,78,85,86,89,90,94,96,110,111,114,118,119,132–135,139,143]

Mesoporos perforatus (Gran) Lillick [= *Exuviella perforata* Gran, *Porella adriatica* Schiller, *P bisimpressa* Schiller, *P. globulus* Schiller, *P. asymmetrica* Schiller, *Porotheca perforata* (Gran) Silva] [58,61,94]

HAB ***Noctiluca scintillans*** (Macartney) Kofoid [= *N. miliaris* Suriray *ex* Lamarck] [7,8,12,18,31,35,36,46,47,51,59–61,75,76,81,94,97,101,110,114,128,129,133–136,141,143]

Oblea rotunda (Balech) Balech *ex* Sournia [= *Peridiniopsis rotunda* Lebour, *Glenodinium rotundum* (Lebour) Schiller, *Diplopsalis rotunda* (Lebour) Wood, *D. rotundata* Steidinger *et* Williams] [9,18,34,59,61,96,110,114]

Oxyphysis oxytoxoides Kofoid [23,59,75,76,137,139]

Oxyrrhis marina Dujardin [= *O. maritima* Van Meel, *O. tentaculifera* Conrad] [58,59,61,143]

Oxytoxum adriaticum Schiller [133]

Oxytoxum brunellii Rampi [133]

Oxytoxum milneri Murray *et* Whitting [= *O. subulatum* Kofoid] [94]

Oxytoxum mitra Stein [1,94]

Oxytoxum parvum Schiller [= *O. tenuistriatum* Rampi, reported as '*O. parvulum*' Schiller] [61]

Oxytoxum variabile Schiller [= *Oxytoxum gracile* Schiller] [61]

Palaeophalacroma unicinctum Schiller [= *Heterodinium detonii* Rampi, *Epiperidinium michaelsarsi* Gaarder] [144]

Cold ***Peridiniella danica*** (Paulsen) Okolodkov *et* Dogde [= *Glenodinium danicum* Paulsen *ex* Braarud pro parte] [9,14,15,18–20,27,34,59,61,88,96,110,114]

Peridiniopsis oculatum (Stein) Bourrelly [= *Glenodinium oculatum* Stein] [61]

Peridiniopsis thompsonii (Thompson) Bourrelly [= *Glenodinium quadridens* (Stein) Schiller, *Peridinium quadridens* Stein] [96]

Peridinium aciculiferum Lemmermann [= *P. umbonatum* var. *aciculiferum* Lemmermann, *P. stagnale* Meunier, *Glenodinium aciculiferum* (Lemmermann) Lindemann] [61,143]

Peridinium bipes Stein [= *P. tabulatum* (Ehrenberg) Claparède *et* Lachmann, *Glenodinium tabulatum* Ehrenberg, *G. apiculatum* Ehrenberg] [34,58,61]

Peridinium cinctum (O.F. Müller) Ehrenberg [= *Peridinium tabulatum* Pénard, *P. cinctum* var. *lemmermannii* West, var. *laesum* Lindemann, var. *regulatum* Lindemann, var. *irregulatum* Lindemann, var. *angulatum* Lindemann, var. *carinatum* Steinecke *et* Lindemann, non var. *gibbosum* Lefèvre, non var. *palustre* Lindemann. Also *P. cinctum* f. *regulatum* (Lindemann) Lefèvre, f. *angulatum* (Lindemann) Lefèvre, f. *ovoplanum* Lindemann, f. *meandricum* Lefèvre, f. *westii* (Lemmermann) Lefèvre, f. *tuberosum* (Meunier) Lefèvre, *P. germanicum* Lindemann, *P. eximium* Lindemann, *P. rhenanum* Lindemann] [9,18,61,84,94,96,143]

Peridinium elpatiewskyi (Ostenfeld) Lemmermann [= *P. umbonatum* var. *elpatiewskyi* Ostenfeld, *P. pygmaeum* Lindemann, *Glenodinium elpatiewskyi* (Ostenfeld) Schiller, *Peridiniopsis elpatiewskyi* (Ostenfeld) Bourrelly] [61]

Peridinium umbonatum Stein [= *Peridinium inconspicuum* Lemmermann, *P. pusillum* (Pénard) Lemmermann, *P. orrei* Huitfeld-Kaas, *P. umbonatum* var. *papilliferum* Lemmermann, *P. javanicum* Bernard, *P. umbonatum* var. *inaequale* Lemmermann, *P. inconspicuum* var. *armatum* Lemmermann, *P. marchicum* Lemmermann, *P. tabulatum* var. *caudatum* Playfair, *P. minimum* Woloszynska, *P. tatricum* Woloszynska, *P. tatricum* var. *spinulosa* Woloszynska, *P. linzium* Lindemann, *P. munusculum* Lindemann, *P. munusculum* f. *spiniferum* Lindemann, *P. caudatum* Playfair, *P. geminum* var. *angulosum* Playfair, *P. geminum* var. *elegans* Playfair, *P. geminum* var. *excavatum* Playfair, *P. marchicum* var. *keyense* Nygaard, *P. steinmannii* Woloszynska, *P. parvulum* Woloszynska, *P. ambiguum* Lindemann, *P. umbonatum* f. *spiniferum* (Lindemann) Lefèvre, *P. inconspicuum* var. *excavatum* (Playfair) Lefèvre, *P. inconspicuum* f. *armatum* (Lemmerman) Lefèvre, *P. inconspicuum* f. *spiniferum* (Lindemann) Lefèvre, *P. africanum* f. *tatricum* (Woloszynska) Lefèvre, *P. africanum* var. *spinulosum* (Woloszynska) Lefèvre, *P. inconspicuum* var. *balatonicum* Entz, *Glenodinium guildfordense* (Playfair) Lindemann, *G. geminum* (Playfair) Lindemann, *G. pusillum* Pénard, *G. lefevrei* Lindemann, *Gymnodinium oligoplacatum* Skuja. Also including *Peridinium umbonatum* var. *lubieniense* (Wolszynska) Popovský *et* Pfeister, *Peridinium lubieniense* Wolszynska, see also Elbrächter & Meyer (2001)] [59,61,143]

Peridinium wulei Huitfeld-Kaas [= *P. ulaum* Garova, *P. glaesrowiense* Lindemann, *P. kincaidi* Wailes, *P. volzii* Lemmermann, *P. tabulatum* Playfair, *P. australe* Playfair, *P. hieroglyphicum* Playfair, *P striolatum* Wailes, *P. vancouverense* Wailes, non *Peridinium tabulatum* (Ehrenberg) Claparède *et* Lachmann] [61,96]

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Table 1. Continued.

Petalodinium porcelio Cachon *et* Cachon [126]

Phalacroma acutum (Schütt) Pavillard [= *P. vastum* var. *acutum* Schütt, *Dinophysis acutoides* Balech, non *D. acutum* Ehrenberg] [61]

Phalacroma favus Kofoid *et* Michener [= *Dinophysis favus* (Kofoid *et* Michener) Abé vel Balech] [6,60]

Phalacroma ovatum (Claparède *et* Lachmann) Jørgensen [= *Dinophysis ovata* Claparède *et* Lachmann] [61,94,135]

Phalacroma parvulum (Schütt) Jørgensen [= *P. porodictyum* Stein var. *parvula* Schütt, *Dinophysis oviformis* Schiller; possible small cell of *D. rotundata* Claparède *et* Lachmann according to Reguera & González Gil (2001)] [60,94,133,134]

Phalacroma pulchellum Lebour [= *Dinophysis pulchella* (Lebour) Balech] [18,61,96,110]

HAB ***Phalacroma rotundatum*** (Claparède *et* Lachmann) Kofoid *et* Michener [= *Dinophysis rotundata* Claparède *et* Lachmann, *P. rudgei* Murray *et* Whitting, *D. whittingae* Balech] [9,15,17–19,20,27,33,34,46,59–61,90,94,96,110,114,119,129,133–135,143,144]

Plectodinium nucleovolvatum Biecheler [= *P miniatum* (Kofoid *et* Swezy) F.J.R. Taylor, *Cochlodinium miniatum* Kofoid *et* Swezy] [94]

Podolampas elegans Schütt [94]

Podolampas spinifera Okamura [61]

Polykrikos kofoidii Chatton [= *P. schwarzii* Kofoid pro parte] [9,132]

Polykrikos schwartzii Bütschli [= *P. auricularia* Bergh] [8,18,42,59,61,94,96,110,114,118,129]

Preperidinium meunieri (Pavillard) Elbrächter [= *Diplopsalis lenticula* Bergh f. *minor* Paulsen, *Zygabikodinium lenticulatum* Loeblich *et* Loeblich III, *Peridinium lenticulum* Mangin, *Glenodinium lenticula* f. *minor* (Paulsen) Pavillard, *Diplopeltopsis minor* (Paulsen) Pavillard] [59,61]

Pronoctiluca acuta (Lohmann) Schiller [128]

Pronoctiluca pelagica Fabre-Domergue [= *Rhynchomonas marina* Lohmann, *Pelagorhynchus marinus* Pavillard] [74,94,128,144]

Pronoctiluca spinifera (Lohmann) Schiller [= *P. tentaculata* (Kofoid *et* Swezy) Fabre-Domergue] [94]

Prorocentrum aporum (Schiller) Dodge [= *P. antarcticum* (Hada) Balech, *Exuviella granii* Gaarder] [59,60,94,133–135]

HAB ***Prorocentrum balticum*** (Lohmann) Loeblich III [= *P. pomoideum* Bursa, *Exuviella baltica* Lohmann, *E. aequatorialis* Hasle] [18,46,60,61,75,76,94,96,110,114,133,134,143]

Prorocentrum compressum (Bailey) Abé *ex* Dodge [= *P. lebourae* Schiller, *Exuviella compressa* Bailey, *E. oblonga* Schiller, *E. lenticulata* Matzenauer, *E. elongata* Rampi] [8,9,14,15,18–20,33,34,46,58–61,63,90,94,96,107,110,114,119,127,133–135,143,144]

HAB ***Prorocentrum cordatum*** (Ostenfeld) Dodge [= *Exuviella cordata* Ostenfeld, *E. pyriformis* Schiller, *?P. minimum* (Pavillard) Schiller] [9–33,42,49,56,58,60,61,63,67–69,72,73,81–87,89,90,94,96–99,105–107,109–112,114–115,118,119,125,129,132–134,137,143]

Prorocentrum dentatum Stein [= *P. obtusidens* Schiller, *P. veloi* Osorio-Tafall, *P. monacense* Kufferath] [60,75,76,94,133,134]

HAB ***Prorocentrum lima*** (Ehrenberg) Dodge [= *Exuviella marina* Cienkowski, *E. caspica* Kisselew, *E. cincta* Schiller, *E. ostenfeldii* Schiller] [18,32,58,59,61,89,94,96,107,110]

Prorocentrum maximum (Gourret) Schiller [= *P. brochii* Schiller] [60,94,133,134,143]

HAB ***Prorocentrum micans*** Ehrenberg [= *P. schilleri* Böhm in Schiller, *P. levantoides* Bursa] [9,14,15,17–20,25–27,30,32,33,46,58–61,75,76,78,79,81,84–86,89,90,94,96,98,99,107,109–111,114,118,119,125,129,132–135,139,143]

HAB ***Prorocentrum minimum*** (Pavillard) Schiller [= *P. mariae-lebourae* (Parke *et* Ballantine) Loeblich III, *P. triangulatum* Martin, *P. cordiformis* Bursa, *?P. cordatum* (Ostenfeld) Dodge] [2,46,59,60,75,76,78,79,94,133,134,138,139]

Prorocentrum obtusum Ostenfeld [9,18,34,61,89,96]

Prorocentrum ovum (Schiller) Dogde [= *Exuviella ovum* Schiller] [94]

Prorocentrum pusillum (Schiller) Loeblich [= *Exuviella pussilla* Schiller, non *P. nanum* Schiller] [58]

Prorocentrum rostratum Stein [= *Prorocentrum styliferum* Lohmann] [75,76]

Prorocentrum rotundatum Schiller [60,94,133–135]

Prorocentrum scutellum Schröder [= *P. sphaeroideum* Schiller, *P. robustum* Osorio-Tafall] [1,12,15,19,20–23,25,28,29,33,34,46,58,60,61,94,96,109,114,119,133–135]

Prorocentrum triestinum Schiller [= *P. redfieldii* Bursa, *P. pyrenoideum* Bursa] [60,133,134]

Prorocentrum vaginulum (Stein) Dodge [= *Dinopyxis vaginula* Stein, *Exuviella vaginula* (Stein) Schütt] [58,61]

Protoceratium areolatum Kofoid [59,60,94,133,134]

HAB ***Protoceratium reticulatum*** (Claparède *et* Lachmann) Bütschli [= *Gonyaulax grindleyi* Reinecke] [9,18,33,34,46,58,59,61,79,90,94,96,110,112,114,119,133,135]

Protoperidinium abei (Paulsen) Balech [= *Peridinium abei* Paulsen, *P. biconicum* Abé, non *P. biconicum* Dangeard] [58]

Protoperidinium achromaticum (Levander) Balech [= *P. finitimum* Balech, *Peridinium achromaticum* Levander] [58,59,61,128,143]

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Table 1. Continued.

Protoperidinium bipes (Paulsen) Balech [= *Minuscula bipes* (Paulsen) Lebour, *Peridinium minusculum* Pavillard, *Glenodinium bipes* Paulsen, non *Peridinium bipes* Stein] [9,18,27,33,34,59,61,94,96,109,110,114,119,128,135,143,144]

Protoperidinium brevipes (Paulsen) Balech [= *Peridinium brevipes* Paulsen, *P. varicans* Paulsen, *P. incurvum* Lindemann] [8,9,18,27,33,34,46,58,60,61,94,96,110,114,119,133–135]

Protoperidinium brochii (Kofoid *et* Swezy) Balech [= *P. adriaticum* Broch, *P. divergens* var. *adriaticum* Schiller] [8,61,90,128]

Protoperidinium claudicans (Paulsen) Balech [= *Peridinium claudicans* Paulsen] [8,60,128,133–135,143]

Protoperidinium conicoides (Paulsen) Balech [= *Peridinium conicoides* Paulsen] [60,61,131,133,134]

Protoperidinium conicum (Gran) Balech [= *Peridinium divergens* var. *conica* Gran] [8,42,59–61,94,128,133–135,143]

HAB ***Protoperidinium crassipes*** (Kofoid) Balech [see Balech (1988: 110) for synonymy with *P. curtipes*] [8,9,18,33–35,59,61,94,96,99,110,119,114,135,143]

Protoperidinium curtipes (Jørgensen) Balech [= *Peridinium curtipes* Jørgensen, *P. crassipes* Paulsen, non Paulsen nec Schiller] [94,128,135]

Protoperidinium curvipes (Ostenfeld) Balech [= *Peridinium curvipes* Ostenfeld] [46,94,135]

Protoperidinium decipiens (Jørgensen) Parke *et* Dodge [= *Peridinium decipiens* Jørgensen] [9,18,58,61,96]

Protoperidinium deficiens (Meunier) Balech [= *Peridinium deficiens* Meunier] [94]

Protoperidinium depressum (Bailey) Balech [= *Peridinium depressum* Bailey] [8,9,18,33–35,46,60,61,94,96,110,113,114,119,128,133–135,143]

Protoperidinium diabolus (Cleve) Balech [= *Peridinium diabolus* Cleve, including *P. longipes* (Karsten) Balech] [8,35,60,61,94,128,133,134,143]

Protoperidinium divergens (Ehrenberg) Balech [= *Peridinium divergens* Ehrenberg] [8,9,18,34,35,46,59–61,94,96,107,114,119,128,133,134,143]

Protoperidinium elegans (Cleve) Balech [= *P. fatulipes* (Kofoid) Balech, *Peridinium annulatum* Kofoid *et* Michener] [8,58,59,61]

Protoperidinium excentricum (Paulsen) Balech [= *Peridinium excentricum* Paulsen, *P. perrieri* Fauré-Frémient] [58,59,61,94,143]

Protoperidinium globulus (Stein) Balech [= *Peridinium ovatum* (Pouchet) Schütt, *P. globulus* var. *ovatum* (Pouchet) Schiller, also *P. globulus* var. *ovatum* (Pouchet) Krachmalny, *P. globulus* var. *quarnerense* (Schröder) Krachmalny] [8,9,18,37,59–61,94,96,114,117,119,128,133,134,143,144]

Protoperidinium grande (Kofoid) Balech [= *P. truncatum* (Graham) Balech] [60,94,133,134]

Protoperidinium granii (Ostenfeld) Balech [= *Peridinium granii* Ostenfeld *ex* Paulsen] [8,9,18,27,34,59–61,79,90,94,96,110,114,119,128,133–135,143]

Protoperidinium inflatum (Okamura) Balech [= *Peridinium inflatum* Okamura, *P. crassum* Dangeard] [128]

Cold *Protoperidinium knipowitschii* (Ussatschew) Balech [= *Peridinium knipowitschii* Ussatschew] [34,59,61,96,143]

Protoperidinium leonis (Pavillard) Balech [= *Peridinium leonis* Pavillard, *P. conicum* Meunier, *P. saltans* Pavillard, *P. striatum* Böhm, *P. leonis* var. *concavilaterale* Kisselew] [8,61,94,128,135]

Protoperidinium longispinum (Kofoid) Balech [= *Peridinium longispinum* Kofoid, *P. michaelis* Ehrenberg pro parte] [9,46,61,89]

Protoperidinium marielebourae (Paulsen) Balech [= *Peridinium obtusum* (Karsten) Lebour, non *P. obtusum* (Karsten) Faure-Fremiet] [94,133]

Protoperidinium minutum (Kofoid) Loeblich III [the synonymy with *P. monospinum* (Paulsen) Zonneveld *et* Dale is debatable] [18,61,96,143]

Protoperidinium oblongum (Aurivillius) Parke *et* Dodge [= *Peridinium oblongum* Cleve, *P. divergens* var. *oblongum* Aurivillius, *P. oceanicum* var. *oblongum* Paulsen, *P. venustum* Matzenauer] [46,94]

Protoperidinium oceanicum (Vanhöffen) Balech [= *Peridinium divergens* var. *oceanicum* Stein] [8,59,61,128,143]

Protoperidinium pallidum (Ostenfeld) Balech [= *Peridinium pallidum* Ostenfeld] [8,9,18,34,46,59,61,94,96,114,128]

Protoperidinium pedunculatum (Schütt) Balech [= *Peridinium pedunculatum* Schütt] [8,61,94,96,143]

Protoperidinium pellucidum Bergh [= *Peridinium pellucidum* (Bergh) Schütt] [8,46,58–61,94,96,109,110,119,133–135,144,143]

Protoperidinium pentagonum (Gran) Balech [= *Peridinium pentagonum* Gran, *P. sinuosum* Lemmermann] [8,33,59–61,94,114,119,128,131,133–135,143]

Protoperidinium punctulatum (Paulsen) Balech [= *Peridinium subinerme* Paulsen var. *punctulatum* (Paulsen) Schiller] [60,94,133,134]

Protoperidinium pyriforme (Paulsen) Balech [= *Peridinium steinii* var. *pyriformis* Paulsen, also *Peridinium breve* Paulsen] [59–61,94,96,119,133–135]

Pacif. *Protoperidinium sinaicum* (Matzenauer) Balech [= *Peridinium sinaicum* Matzenauer] [8,61]

Continued on p. 52

Table 1. Continued.

	Protoperidinium solidicorne (Mangin) Balech [= *P. spiniferum* (Schiller) Balech, *P. spinosum* Schiller] [8,9,18,34,35,46,58,59,61,94,96,110,114,128,131,135,143]
	Protoperidinium steinii (Jørgensen) Balech [= *P. steinii* Jørgensen, *P. michaelis* Stein] [1,8,9,18,25,33,34,46,59–61,90,94,96,107,110,111,113,114,119,128,133,134,143,144]
	Protoperidinium subinerme (Paulsen) Loeblich III [= *Peridinium subinerme* Paulsen] [58–61,94,128,133–135]
	Protoperidinium thorianum (Paulsen) Balech [= *Peridinium thorianum* Meunier, *Glenodinium thorianum* Paulsen] [59]
	Ptychodiscus noctiluca Stein [= *P. inflatus* Pavillard, *P. carinatus* Kofoid] [59]
	Pyrocystis elegans Pavillard [60,133,134]
	Pyrocystis lunula (Schütt) Schütt [= *Gymnodinium lunula* Schütt] [8,61,81]
	Pyrophacus horologium Stein emend. Wall *et* Dale [9,18,59–61,94,96,110,114,119,133,134,143]
	Pyrophacus steinii (Schiller) Wall *et* Dale [= *P. horologicum* var. *steinii* Schiller] [94,135]
	Scaphodinium mirabile Margalef [= *Leptospathium navicula* Cachon *et* Cachon] [126]
HAB	***Scrippsiella trochoidea*** (Stein) Balech *ex* Loeblich III [= *Peridinium trochoideum* (Stein) Lemmermann, *P. faeroense* Paulsen, *Scrippsiella sweeneyae* Balech *ex* Loeblich III] [8,9,18,21–23,27,28,34,41,46,58–61,75,76,86,89,94,96,114,133–137,139,143]
	Spatulodinium pseudonoctiluca (Pouchet) Cachon *et* Cachon *ex* Loeblich *et* Loeblich III [= *Gymnodinium pseudonoctiluca* Pouchet] [126]
	Torodinium robustum Kofoid *et* Swezy [= *Gymnodinium teredo* Schütt pro parte] [61]
	Woloszynskia neglecta (Schilling) R.H. Thompson [= *Gymnodinium neglectum* (Schilling) Lindemann, *Glenodinium neglectum* Schilling] [59]

of the eutrophication. However it is likely that these species remained unnoticed in previous studies.

Cold waters species: Arctic-boreal affinities?

The low species richness could be associated with the low temperatures in the Black Sea (<4 °C in winter) that only favour cryophilic or eurythermal species. The Arctic Seas with 95 and 189 species listed in the Canadian and Russian waters, respectively (Hsiao, 1983; Okolodkov, 1998) also present low species richness compared to temperate or warm oceans.

Most of the freshwater taxa (from continental waters; Popovský & Pfiester, 1990) can be considered as cryophilic/eurithermal species, being here discarded for marine biogeography. Athecate species such as *Amphidinium longum* Lohmann (= *A. acutum* Lohmann), *A. extensum* Wulff, *A. ovum* Herdman (sand-living), *Gyrodinium britannicum* Kofoid *et* Swezy and also *Gymnodinium wulffii* Schiller are reported from the cold waters of the North Atlantic Ocean, but not or rarely reported in the Mediterranean waters (Gómez, 2003).

Okolodkov & Dodge (1996) reported only four Arctic-boreal species, *Alexandrium ostenfeldii* (Paulsen) Balech *et* Tangen, *Amylax triacantha* (Jörgensen) Sournia, *Ceratium arcticum* (Ehrenberg) Cleve, *Dinophysis norvegica* Claparède *et* Lachmann and the bi-polar *Dinophysis arctica* Meresch-kowsky, *Protoperidinium islandicum* (Paulsen) Balech, *P. saltans* (Meunier) Balech and *P. thulesense* Balech. All these species except *C. arcticum* and the last three are reported from the Black Sea. The records of Arctic-boreal species proposed by Okolodkov & Dodge (1996) are scarce and/or dubious in the Mediterranean Sea (Gómez, 2003).

Dinophysis arctica, *D. norvegica* and *D. apiculata* Meunier are not or rarely reported in the Mediterranean waters (Gómez, 2003). Similarities have been reported in the developmental stages of *D. acuminata*, *D. acuta* and *D. norvegica* (e.g., Reguera & González Gil, 2001). Genetic analyses showed that *D. acuminata* and *D. norvegica* were nearly identical (>99%) (Rehnstam-Holm et al., 2002). *D. apiculata*, reported only by Krakhmalny (1994) in the Black Sea, is according to Okolodkov (1998) related to *D. acuminata*. *Dinophysis apiculata* presented only one record in the Mediterranean Sea (Gómez, 2003).

Amylax triacantha only presents one dubious record in the Mediterranean Sea and *Alexandrinum ostenfeldii* is reported from the Egyptian waters (Gómez, 2003). Other thecate species that can be considered as cryophilic are *Gonyaulax cochlea* Meunier, *Protoperidinium knipowitschii* (Ussatchev) Balech, *Protoperidinium deficiens* and *Peridiniella danica* (Paulsen) Okolodkov *et* Dodge. *P. knipowitschii* is

rather similar in shape to the cosmopolitan species *Protoperidinium grande* (Kofoid) Balech [Taylor, 1976: 150] or to the bi-polar *P. saltans* (Meunier) Balech [Balech, 1974: 64] as well as *Peridinium fatulipes* Kofoid [Kisselew, 1950: 203]. *P. deficiens*, with one dubious record from the Mediterranean Sea (Gómez, 2003), could be considered a cold water species. *Peridiniella danica*, typically known from the North Atlantic Ocean (Okolodkov & Dodge, 1995), is reported from the North Adriatic Sea (Viličić et al., 2002) with additional, doubtful, records from the warm waters of the southern Mediterranean basin (Dowidar, 1974; Skolka et al., 1986). *Ceratium longipes* (Bailey) Gran (= *C. arcticum* var. *longipes* (Bailey) Graham *et* Bronikovsky) seems to be more common in cold waters (Okolodkov & Dodge, 1996).

Indo-Pacific species?

A reduced group of species not reported in the Atlantic Ocean to the best of our knowledge, but in the Indian and/or Pacific waters, includes dubious Indo-Pacific species such as *Amphidinim cucurbita* Kofoid *et* Swezy, *Gymnodinium radiatum* Kofoid *et* Swezy (recently reported by Krakhmalny, 2001) and *G. sulcatum* Kofoid *et* Swezy (Mediterranean; Gómez 2003). Among thecate dinoflagellates the only reports are of *Protoperidinium sinaicum*, which resembles to *Protoperidinium tuba* (Schiller) Balech, both doubtful or insufficiently known taxa (Taylor, 1976: 160).

Non-Mediterranean taxa and/or introduced species?

Nearly all the species reported from the Black Sea (Table 1) are also reported from the Mediterranean Sea. Several exceptions were *Amphidinium conradii* Schiller, *A. ovum* Herdman [both from the North Atlantic Ocean; Parke & Dodge (1976)], *Cochlodinium citron* Kofoid *et* Swezy [doubtful record by Skolka et al. (1986) in the Mediterranean Sea] as well as the Atlantic species *Cochlodinium pirum* (Schütt) Lemmermann. Excluding these dubious records only *Alexandrium monilatum* (Howell) Balech remains as a non-Mediterranean taxon, together with several Artic-boreal species and *A. cucurbita* and *G. radiatum* as artificially Indo-Pacific taxa.

Alexandrium monilatum, responsible for blooms in the Black Sea since 1991 (Moncheva et al., 2001a), is typically known from sub- and tropical regions of the Atlantic and Eastern Pacific Ocean, although it was also recorded in the cold waters of the Chesapeake Bay (Steidinger & Tangen, 1997: 499). Live cells of *A. monilatum* are easily identifiable compared to congeneric species, but difficult from fixed samples. A dubious record, as *Gessnerium mochimaensis* Halim *ex* Halim, is reported from the Suez Canal in the summer (El-Sherif & Ibrahim, 1993). It is unusual the proliferation of this taxon, an *a priori* thermophilic species, in the cold waters of the Black Sea.

The exchange of species, toxic or not, between the Mediterranean and Black Seas seems to be rare. Despite *A. monilatum* is being reported from Bulgarian waters close to the Bosphorus/Dardanelles Straits, the introduction to the Mediterranean Sea, favoured by the westward surface current system, is not reported. For example *Karenia brevis* (Davis) G. Hansen *et* Moestrup, a common toxic species in the Aegean Sea eutrophic waters (Gotsis-Skretas & Frigilos, 1990), is not reported in the Black Sea. Moncheva et al. (2001b) reported that despite the fact that the Aegean Sea, like the Black Sea, could be considered a eutrophic basin, the bloom-forming assemblages show a low taxonomic similarity. This has been attributed to both natural factors and dissimilarities and to the gradients in nutrient levels and their ratios (Moncheva et al., 2001b).

As non-indigenous plankton species (introduced species) from the Black Sea, Moncheva & Kamburska (2002) listed *Gymnodinium uberrimum* (Allman) Kofoid *et* Swezy, *Oxyphysis oxytoxoides* Kofoid, *Gymnodinium fuscum* (Ehrenberg) Stein, *Gyrodinium* cf. *aureolum* Hulburt, 'Gyrodinium simplex', *Spatulodinium pseudonoctiluca*, *Scaphodinium mirabile*, *Petalodinium porcelio* as well as *Alexandrium monilatum*.

Red tides by the freshwater species *Gymnodinium uberrimum* were reported from the western Black Sea since 1990's (Moncheva et al., 2001a). However this taxon presents a high number of related species or synonyms indicative of its difficult identification (Popovský & Pfiester, 1990: 117). As reported in Wyatt & Carlton (2002) *G. uberrimum* is a common bloom-forming species in European and North American lakes and its appearance in estuarine areas of the Black Sea is not unexpected.

Moncheva & Kamburska (2002) reported a possible origin of *Oxyphysis oxytoxoides* from Alaska/California. However this species was reported from the Mediterranean (Gómez, 2003), recently from the Marmara Sea (Balkis, 2000) and all major oceans (Sournia, 1986: 44). *Gymnodinium fuscum* is primarily a freshwater taxon of difficult identification, with dubious records in the Mediterranean Sea (Gómez,

2003). More uncertainties appear with *Gymnodinium aureolum* (Hulburt) G. Hansen related to the *Gymnodinium mikimotoi* complex (Hansen et al., 2000). *Gymnodinium simplex* (Lohmann) Kofoid *et* Swezy is also a species of complex identification frequently reported in the Mediterranean Sea (Gómez, 2003).

Stoyanova (1999) reported for the first time the noctilucaceans *Spatulodinium pseudonoctiluca*, *Scaphodinium mirabile* and *Petalodinium porcelio* in the Black Sea. *S. pseudonoctiluca* is reported from all major oceans (Sournia, 1986: 52). These three taxa, and especially the leptodiscaceans, *S. mirabile* and *P. porcelio*, strongly differ from the typical appearance of the dinoflagellates (Peridiniales) and that, together with the scarcity of available literature, is responsible for the under-estimation of these ubiquitous species, going unnoticed under routine microscopical analysis. For example *S. mirabile* is reported from the Mediterranean Sea (Gómez, 2003), Atlantic Ocean (Margalef, 1973) also recently from the Marmara Sea (Balkis, 2000). *S. mirabile* and *P. porcelio* can be found in the western Pacific Ocean (F. Gómez, unpublished results).

Exclusively Mediterranean–Black Sea species

Several species seem to be restricted to the Mediterranean–Black Sea waters such as several inappropriately described unarmored taxa: *Gymnodinium najadeum* Schiller, *G. neapolitanum* Schiller and *G. semidivisum* Schiller. The aberrant dinoflagellate *Petalodinium porcelio* Cachon *et* Cachon (Stoyanova, 1999) can be considered exclusively a Mediterranean–Black species, but probably this taxon remains unnoticed in the world's oceans. The citation of the thecate *Gonyaulax elegans* Rampi constitutes the only worldwide record of this dubious species never reported after the initial description in the Mediterranean Sea (Gómez, 2003). Many of the species of the genus *Gonyaulax* Diesing described by Rampi are considered as synonyms of other congeneric species (see Dodge & Saunders, 1985).

Endemic species?

The geologic evolution of the Ponto–Caspian basins involved a succession of separations/isolations and in more recent geologic time the reconnection to the ocean (Mediterranean Sea) (e.g., Mudie et al., 2002). These events resulted in the evolution of diverse modern organism assemblages of freshwater, brackish water, and marine taxa of mixed origins consisting of endemic (autochthonous) Ponto–Caspian species, Mediterranean–Atlantic immigrants, and Arctic Pleistocene glacial relicts. For macroscopic organisms, the autochthonous Ponto–Caspian species are characterized by wide adaptive capacities and constitute a significant portion of the invasive species currently spreading to regions in northern Europe and to the Great Lakes (Reid & Orlova, 2002). In the semi-enclosed Black Sea, with special hydrological, chemical and trophic conditions, a high endemism by Ponto–Caspian relict algal species could be expected.

A candidate could be *Prorocentrum caspicum* (Kisselew) Krakhmalny described from the Caspian Sea and further from the Arctic Sea (Kisselew, 1950). However this taxon is considered a synonym of *Prorocentrum lima* (Ehrenberg) Dodge (Dodge, 1975). *Prorocentrum cordatum* (Ostenfeld) Dodge originally described from the Caspian Sea is considered endemic and prominent in the Ponto–Caspian basins (Makarova, 1969), but the cosmopolitan *Prorocentrum minimum* (Pavillard) Schiller is considered to be synonym (Marasović et al., 1990; Velikova & Larsen, 1999). Several morphological varieties (infraespecific taxa) such as *Prorocentrum cordatum* var. *aralensis* (Kisselew) Krakhmalny or *Amphidinium klebsii* f. *ponticum* Rouchijajnen are reported (Kisselew, 1950; Krakhmalny, 1994). In conclusion, no taxa can be recognized as endemic species.

Final remarks

The extreme environmental conditions (high nutrient concentrations and modified nutrient ratios) are associated with low species richness and dominance of mono-specific blooms such as *Noctiluca scintillans*, *Prorocentrum cordatum*, *Heterocapsa triquetra*, *Scrippsiella trochoidea* (Stein) Balech *ex* Loeblich III, among others (Bologa et al., 1995; Mihnea, 1997; Velikova et al., 1999). Compared to the Mediterranean waters, several cold-water species appeared, indicative of the Arctic Seas affinities or the presence of glacial period relicts. Despite the strong environmental modifications that could favour invasive species in competition for niches, it is difficult to establish a tentative list of introduced species. The non-indigenous species list proposed by Moncheva & Kamburska (2002) is composed of doubtful taxa and species unnoticed in previous studies and/or taxa recently recognized at species level. More in deep taxonomical studies, with the application of recent taxonomical approaches, are

necessary to establish the species richness in the Black Sea waters.

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ORIGINAL ARTICLE

Endemic and Indo-Pacific plankton in the Mediterranean Sea: a study based on dinoflagellate records

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ABSTRACT

Aim To investigate biogeographical patterns based on published dinoflagellate records from the Mediterranean and Black Seas, and to provide a tentative list of endemic and Indo-Pacific dinoflagellates in the Mediterranean Sea.

Location Mediterranean Sea, Black Sea.

Methods Checklists of dinoflagellates of the Mediterranean and Black Seas were compared with worldwide literature records. Only species reported in the Indo-Pacific Ocean or exclusively known in the Mediterranean Sea were selected for biogeographical analysis.

Results Dinoflagellates in the Mediterranean Sea comprised *c.* 43% of the world marine species and *c.* 88% of the dinoflagellate genera. Species richness among the Mediterranean sub-basins showed marked differences due to the less reliable records of unarmoured (athecate) and rare dinoflagellates. These differences disappeared when only the more easily identifiable taxa were considered. Of the 673 dinoflagellates cited in the Mediterranean, 87% were also reported in the Atlantic Ocean. Only 40 taxa (6% of the total) were considered to be potential Indo-Pacific species. Most were reported from the Ligurian Sea (21), and only two species from the Levantine basin. The other 48 taxa (7% of total) were known exclusively from the Mediterranean Sea, mainly from the Ligurian Sea. Half of these taxa were reported by a single author.

Main conclusions Substantial dinoflagellates species richness can be attributed, in part, to the historical tradition of taxonomic studies in the Mediterranean Sea. The list of species of both Indo-Pacific and exclusively Mediterranean species included taxa of dubious taxonomic validity or that were insufficiently known. The exclusion of these questionable taxa revealed the near absence of endemic dinoflagellates in the Mediterranean Sea compared with macroscopic organisms. This could be related to: (1) continuous replenishment of the plankton populations by the inflow of Atlantic water through the Strait of Gibraltar, (2) the possibility that species introduced during the Pliocenic flooding after the Messinian salinity crisis have not had enough time to diverge from their Atlantic ancestors, and/or (3) the reliance on traditional taxonomy based on morphological characters, which precludes the detection of cryptic speciation.

Keywords

Black Sea, dinoflagellate, endemic, Erythrean invader, Indo-Pacific, Lessepsian migrant, marine biogeography, Mediterranean Sea, phytoplankton.

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INTRODUCTION

It has been estimated that *c.* 26% of the total Mediterranean marine fauna (4238 species, Fredj *et al.*, 1992) are endemic. This rich biodiversity represents 4–18% of the total number of species in the world's oceans (Fredj *et al.*, 1992; Bianchi & Morri, 2000). The generally high biodiversity of the Mediterranean Sea may be explained by the synergy of: (i) a

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historical tradition of taxonomic studies, (ii) a wide variety of climatic and hydrographic conditions, and (iii) the fluctuating hydrography of the Mediterranean Sea on a geological scale as communication with the Atlantic and Indian Oceans opened and closed due to changing sea levels and plate tectonics, serving as a type of 'diversity pump' (Fredj *et al.*, 1992; Bianchi & Morri, 2000).

The biodiversity of the Mediterranean Sea is undergoing rapid alteration within the context of a globally changing climate (Jeftič *et al.*, 1992; Bianchi & Morri, 2000). The basin has been subject to introductions of non-indigenous species by ship traffic since the opening of maritime routes five centuries ago. Since 1869 a narrow, man-made channel has connected the Mediterranean and the Indian Ocean: the Suez Canal has been considered the major gateway for the entry of invading species, and over 300 Erythrean species have established populations (Galil, 2000). This northbound migration of Erythrean invaders, formerly Lessepsian migrants, appears to have been accelerated during the past few decades by a rise in the sea temperatures as well as by the activation of the Aswan High Dam, leading to more oligotrophic conditions on the Mediterranean side of the Canal (Por, 1990). Exotic macrophytes, invertebrates and fish are found in most coastal habitats in the Mediterranean Sea. In addition to the Erythrean invaders, species are intentionally or accidentally introduced into the Mediterranean via ship fouling, ballast waters, aquaculture, trade in living bait, wrapping of fresh seafood in living algae, aquariology, and scientific research (Bianchi & Morri, 2000).

The Mediterranean Sea is a remnant of the extensive Tethys Ocean of the Triassic (*c.* 200 Ma BP). During the Cretaceous (*c.* 120 Ma BP), the Mediterranean was opened to communication with the Atlantic Ocean. Later in the Miocene (*c.* 10 Ma BP), the isthmus of Suez was formed, isolating the Mediterranean from the Indo-Pacific Ocean. Towards the end of the Miocene, the connection with the Atlantic Ocean closed again as the Messinian salinity crisis led to nearly complete evaporation of the sea. The Messinian salinity crisis occurred synchronously throughout the Mediterranean Basin *c.* 5.96 Ma BP, and caused a large fall in sea level (> 1000 m). The Messinian salinity crisis ended 5.33 Ma BP, during the Pliocene, with the reopening of the Strait of Gibraltar (Krijgsman *et al.*, 1999) which inundated the Mediterranean Basin in only 35 years (Blanc, 2002). During the Quaternary, the alternating ice ages and warm interglacial periods resulted in repopulation of the Mediterranean with boreal or subtropical species, respectively, of Atlantic origin. Bianchi & Morri (2000) separated the present marine biota into several biogeographical categories: (1) temperate Atlantic–Mediterranean, (2) cosmopolitan/panoceanic, (3) endemic, palaeoendemic (Tethyan origin) and neoendemic (Pliocenic origin), (4) subtropical Atlantic (interglacial remnant), (5) boreal Atlantic (ice-age remnants), (6) Red Sea migrants, and (7) eastern Atlantic migrants (especially in the Alborán Sea). Exchange through the Strait of Gibraltar can be considered the main source of species to the Mediterranean Sea, excluding the Tethys relics that survived the extreme environmental changes associated with the Messinian salinity crisis. Fredj *et al.* (1992) reported that 67% of the Mediterranean fauna (excluding protists) were also known from the Atlantic Ocean.

The introduction of exotic species modifies the ecosystem: endemic species unable to tolerate this perturbation will go extinct and exotic species will flourish. Studies of this dilemma require characterization of the marine biota. Studies on Mediterranean biogeography are numerous, but nearly all are focused on macroscopic organisms, whereas studies on the biogeographical affinities of marine phytoplankton are almost non-existent. Halim (1990) reported a list of Indo-Pacific dinoflagellates. Marino (1990) concluded that it is difficult at present to quantify the number of endemic phytoplankton species.

Several authors link the changing nitrogen–silicon ratio in the Mediterranean Sea to a large increase in the number of blooms of phytoplankton species that do not require silica for their growth (a shift from diatoms to dinoflagellates) (Turley, 1999). More than 200 dinoflagellate species have a negative impact on human activity through the production of potent toxins which may accumulate in the food chain (red-tides or harmful algal blooms) (Sournia, 1995). In terms of species richness, the number of species of dinoflagellates is comparable only to that of diatoms. About 1500 diatoms (Sournia *et al.*, 1991) and 1555 dinoflagellate species comprise the marine phytoplankton in the world's oceans (Gómez, 2005).

The aims of this study are to establish the biogeographical origin of the Mediterranean dinoflagellates, and to present a checklist of species candidates considered to be endemic or Indo-Pacific taxa. The validity of these species and the low endemism compared with macroscopic groups are discussed.

METHODS

A matrix was constructed based on the checklist of dinoflagellates reported by Gómez (2003a) for each Mediterranean sub-basin, and by Gómez & Boicenco (2004) for the Black Sea. The distribution of each taxon in the world's seas was established from scrutiny of more than 1100 references. Only some references of interest are cited due to space limitations.

The species cited in the Atlantic waters were eliminated as potential endemic or Indo-Pacific taxa. The remaining group of species was divided into: (1) exclusively Mediterranean species, potential candidates as endemic species, and (2) Indo-Pacific species known exclusively from the Mediterranean and Indo-Pacific Basins.

RESULTS AND DISCUSSION

Dinoflagellates recorded from the Mediterranean Sea comprise 673 species (104 genera), a value close to the 660 species previously reported by Marino (1990) (this author did not report a species checklist). Sournia *et al.* (1991) reported that 1424–1772 species comprising *c.* 115–131 genera constitute the dinoflagellates in the world's oceans. Gómez (2005) listed 1555

species and 117 genera. Thus, although the Mediterranean represents only a small percentage of the world's ocean (0.82% by surface area and 0.32% by volume), nearly 43% of the world's marine dinoflagellate species occur there, including *c.* 88% of the dinoflagellate genera. This percentage is higher than the average value of 6.3% (4–18%) for marine macroscopic organisms in the Mediterranean Basin (Bianchi & Morri, 2000).

The species richness of dinoflagellates in the Mediterranean Basin is highly variable among its sub-basins. In the Ligurian Sea, the smallest of the Mediterranean sub-basins, 74% of the total species have been reported. The number of species cited in the Ligurian and Ionian Seas compared with other sub-basins (Alborán or Aegean Seas) substantially increases when the less reliable records of unarmoured (athecate) dinoflagellates are included. Innamorati *et al.* (1986, 1989a,b) and Skolka *et al.* (1986) cited many freshwater species and synonyms considered as separate species for the Ligurian and Ionian Seas, respectively. Also suspect among the armoured (thecate) dinoflagellates are the large number of species of *Histioneis* Stein, *Heterodinium* Kofoid and, to a lesser extent, *Oxytoxum* Stein and *Gonyaulax* Diesing, cited in the Ligurian Sea. Many of the species described by Rampi (see references in Rampi & Bernhard, 1980) and Halim (1960) have not been reported after the initial descriptions (Gómez, 2003a). These rare taxa and unarmoured forms accounted for the variable distribution of species among the Mediterranean sub-basins (Fig. 1). These unreported taxa should be interpreted as having been overlooked by non-specialist authors and/or due to the scarcity of taxonomic studies in these sub-basins, rather than as being absent.

More easily identifiable genera, such as *Ceratium* Schrank, have been the subject of several biogeographical studies (e.g. Dodge & Marshall, 1994). In the eastern Mediterranean basin, the Aegean Sea, with only half the total species richness reported in the Ionian or Adriatic Seas, had more records of *Ceratium* species than either of the aforementioned sub-basins (Gómez, 2003a). In the Alborán Sea, with about one-third of the total species cited in the Ligurian Sea, 46 species of *Ceratium* were reported, as opposed to the 52 species of the Ligurian Sea (Gómez, 2003a). If the more difficult-to-recognize unarmoured forms and dubious taxa are disregarded, the species richness for each sub-basin is quite similar. For example, the Levantine Basin shows greater species richness than the Adriatic or Ionian Seas. High species richness in some Mediterranean sub-basins is probably due to the unequal number of studies, rather than true differences in species richness among the sub-basins.

Indo-Pacific species

Since the Miocene, communication between the eastern Mediterranean (Tethys Sea) and the Indian Sea has been closed (Maldonado, 1985). A narrow, man-made channel connecting the Mediterranean with the Red Sea was opened during the Egyptian Empire period (Sneh *et al.*, 1975). Since the completion of the Suez Canal in 1869, Erythrean species have colonized the Mediterranean marine biota (Por, 1978). It has been calculated that these species (over 300) now constitute nearly 5% of the global Mediterranean fauna and 13% of the species found in the Levantine Basin (Fredj *et al.*, 1992; Galil, 2000).

The 168 km of the Suez Canal are characterized by extreme physical and chemical conditions: high turbidity, high temperatures, and two salinity barriers represented by the hypersalinity of the Bitter Lakes in the south and the Nile freshwater dilution at the north. The residual current tends to flow from the Red Sea for 10 months, reversing in late summer. The completion of the Aswan High Dam in 1965, and the increase of the cross-sectional flow, have minimized the two salinity barriers. The progressive increase of the water fluxes (and reduction of the salinity gradients) could favour northbound migration directly through the Suez Canal (Halim, 1990). Ships navigating the Canal may likewise facilitate migration of species via transport in their ballast waters (Shefer *et al.*, 2004).

From the 673 species of free-living dinoflagellates listed by Gómez (2003a), 40 species (6% of the total) were cited exclusively from the Mediterranean Sea and Indo-Pacific Ocean (Table 1). Most of the taxa were reported from the Pacific Ocean, and only 11 species from the Indian Ocean. In this case the low number of studies in the Indian Ocean

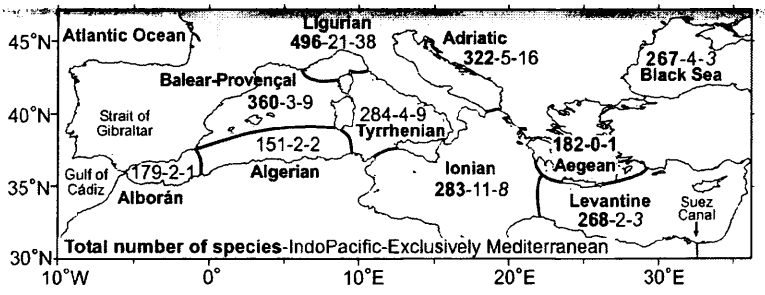

Figure 1 Map of the Mediterranean sub-basins and the Black Sea. Number of dinoflagellate species cited in each Mediterranean sub-basin and the Black Sea based on Gómez (2003a); Gómez & Boicenco (2004); number of dinoflagellate species tentatively considered as Indo-Pacific taxa (see Table 1 for species list); number of exclusively Mediterranean dinoflagellates (see Table 3 for species list).

Table 1 Species reported only in Mediterranean and Indo-Pacific waters

Alexandrium insuetum Balech (Tyr)	*Gymnodinium ovulum* Kofoid & Swezy (Lig)
**Amphidinium curvatum* Schiller† (Lig, Ion, Adr, BS)	*Gymnodinium ravenescens* Kofoid & Swezy (Lig)
**Amphidinium inflatum* Kofoid† (Alg)	*Gymnodinium sphaeroideum* Kofoid (Lig, Ion)
**Amphidinium lissae* Schiller‡ (Lig, Adr)	*Gymnodinium translucens* Kofoid & Swezy (Lig)
**Amphidinium vasculum* Kofoid & Swezy† (Ion)	*Gyrodinium acutum* (Schütt) Kofoid & Swezy (Bal, Tyr, Ion)
Amphidoma elongata Kofoid & Swezy (Alb, Alg)	*Gyrodinium biconicum* Kofoid & Swezy (Ion)
Amphisolenia complanata Kofoid & Skogsberg (Lig)	*Gyrodinium rubricaudatum* Kofoid & Swezy (Lig)
Centrodinium elongatum Kofoid (Alb)	**Heterodinium crassipes* Schiller† (Adr)
**Ceratium egyptiacum* Halim (Lev)	*Heterodinium dubium* Rampi¶ (Lig)
Ceratoperidinium yeye Margalef (Alb, Bal, Lev)	*Histioneis detonii* Rampi¶ (Lig)
Cochlodinium turbineum Kofoid & Swezy (Adr)	**Histioneis elongata* Kofoid & Michener (Lev)
Craspedotella pileolus Kofoid (Lig)	*Leptodiscus medusoides* Hertwig (Bal, Lig, Tyr)
**Gonyaulax ligustica* Rampi§ (Bal, Lig)	**Oxytoxum areolatum* Rampi§ (Bal, Ion, Adr)
Gonyaulax rugosum Wailes (Ion)	*Parahistioneis acutiformis* Rampi¶ (Lig)
Gymnodinium attenuatum Kofoid & Swezy (Lig, Ion)	*Petalodinium porcelio* Cachon & Cachon (Lig)
Gymnodinium canus Kofoid & Swezy (Ion)	*Protoceratium pepo* Kofoid & Michener (Lig)
Gymnodinium lineatum Kofoid & Swezy (Ion)	*Protoperidinium tregouboffii* (Halim) Balech (Lig)
Gymnodinium lira Kofoid & Swezy (Lig)	*Scrippsiella precaria* Montresor & Zingone** (Tyr, Ion)
**Gymnodinium multilineatum* Kofoid & Swezy†	*Triposolenia longicornis* Kofoid (Lig)
**Gymnodinium sulcatum* Kofoid & Swezy† (also BS)	*Warnowia pulchra* Schiller** (Tyr, Lig)

*Taxa cited in the Indian Ocean. Alb, Alborán; Alg, Algerian; Bal, Balear-Provençal; Lig, Ligurian; Tyr, Tyrrhenian; Ion, Ionian; Adr, Adriatic; Aeg, Aegean; Lev, Levantine; BS, Black Sea.

†From Australian waters (Wood, 1963a,b).

‡From the Red Sea (Halim, 1969).

§From the Arabian Gulf (Dorgham & Moftah, 1986).

¶Only reported in the south Pacific Ocean (Rampi, 1948, 1950).

**Reported in the Pacific Ocean (Chihara & Murano, 1997).

compared with other major oceans should be taken into account.

Most of the Mediterranean Indo-Pacific dinoflagellates corresponded to taxa described by Kofoid and collaborators (Kofoid & Michener, 1911; Kofoid & Swezy, 1921; Kofoid & Skogsberg, 1928) from the eastern Pacific Ocean (Table 1). This literature is commonly referenced for the identification of Mediterranean species, and many authors working in the Mediterranean have assigned their observations to the Pacific taxa illustrated by Kofoid. For unarmoured dinoflagellates, despite the excellent and detailed descriptions by Kofoid & Swezy (1921) compared with other, older studies, poor fixation due to the commonly used preservatives formaldehyde and iodine hindered identification. With these preservatives, body shape and morphology often change during the process of fixation so that even determination of the genus becomes difficult (Steidinger & Tangen, 1997).

The list of Mediterranean Indo-Pacific taxa is full of dubious or poorly known species. *Ceratium egyptiacum* Halim was reported as an example of a recent Erythrean invader (Halim, 1990). The taxon shows variable morphology associated with the stress of environmental changes (salinity > 47) in the Suez Canal (Dowidar, 1972). *Ceratium egyptiacum*, which resembles *Ceratium pulchellum* Schröder, was reported only from the proximity of the Suez Canal, with no records in the Indian or Pacific Oceans. *Alexandrium insuetum* Balech is recognizable only by a few specialists; Steidinger & Tangen (1997) reported differences in the sulcal plates between the Mediterranean and Pacific specimens. *Gonyaulax ovalis* Schiller and *Gonyaulax ovata* Matzenauer may be synonyms, and both taxa are dubious. The description of *Gonyaulax rugosum* Wailes was insufficient. *Protoperidinium tregouboffii* Halim was reported only by Balech (1962) in the Pacific Ocean. This taxon shows similarity to the cosmopolitan *Protoperidinium brachypus* (Schiller) Balech. *Ceratoperidinium yeye* Margalef (= *C. mediterraneum* Abbud Abi-Saab) has recently been reported from the Pacific Ocean (Gómez *et al.*, 2004). This taxon may be overlooked in other oceans. Halim (1969) reported *Pyrodinium bahamense* var. *compressum* (Böhm) Steidinger, Tester *et* Taylor (formerly *P. schilleri* (Matzenauer) Schiller) from Port Said, just on the Mediterranean side of the Suez Canal; however no other Mediterranean records exist of this distinctive taxon, which has been investigated extensively due to its toxicity. The Noctilucales Haeckel *Petalodinium porcelio* Cachon & Cachon and *Leptodiscus medusoides* Hertwig have been found recently in Pacific waters (Gómez & Furuya, 2005). These taxa are barely recognizable as dinoflagellates, and are probably going unnoticed in the world's oceans (Gómez & Furuya, 2004, 2005). For *Craspedotella* Kofoid, the record by Cachon & Cachon (1969) in the Mediterranean Sea differed from the description by Kofoid from the Pacific Ocean.

In the Black Sea, it is doubtful that *Amphidinium cucurbita* Kofoid *et* Swezy, *Gymnodinium radiatum* Kofoid & Swezy, *Gymnodinium sulcatum* Kofoid & Swezy and *Protoperidinium*

sinaicum (Matzenauer) Balech belong to Indo-Pacific taxa (Gómez & Boicenco, 2004).

The absence of information on dinoflagellates before the opening of the Suez Canal hinders attempts to determine the biogeographical origins of present Mediterranean species. According to Marino (1990), tropical invaders from the Red Sea only partially compensate for the lack of Atlantic species in the eastern Mediterranean Sea. Since the highest number of Indo-Pacific macroscopic species occurred in the Levantine basin (Galil, 2000), it is expected that, likewise, a majority of Indo-Pacific dinoflagellates would occur here. In the Levantine basin only the doubtful taxon *C. egyptiacum* and *Histioneis elongata* (the latter illustrated by Polat & Koray, 2002) remain as Indo-Pacific dinoflagellates. Most of these tentative Indo-Pacific dinoflagellates, however, were reported from the Ligurian Sea (21 species) (Fig. 1). The present study did not find any clear candidate Indo-Pacific species. Curiously, the toxic and distinctive dinoflagellate *Dinophysis miles* Cleve, a solid example of an Indo-Pacific species, frequently occurring even in the Red Sea, has never been reported in the Mediterranean Sea.

Halim (1990) reported a tentative list of 17 armoured Mediterranean–Indo-Pacific dinoflagellates. However the Indo-Pacific origin of these species is questionable due to the fact they were also reported in the Atlantic Ocean. Furthermore, several of the species are dubious or invalid taxa (Table 2).

According to Por (1978), Red Sea species in the Levantine Basin will increase and decline according to future climatic fluctuations. The increase of temperature and salinity in the Mediterranean Sea, associated with climate change, could facilitate the adaptation of introduced Red Sea/Indian Ocean species. The Strait of Gibraltar is another route for the entrance of tropical species. For example, *Gymnodinium catenatum* Graham, a distinctive toxic dinoflagellate, has apparently entered the Mediterranean Sea through the Strait of Gibraltar (Gómez, 2003b). Global warming is expected to promote northward expansion of tropical species in the eastern Atlantic towards the Strait of Gibraltar. Studies on the phytoplankton composition along the coasts of Africa and the Alborán and Algerian Seas are nearly non-existent, precluding the detection of tropical phytoplankton species entering the Mediterranean Sea from the Atlantic. As most monitoring studies are carried out along the Italian coasts or in the north-west Mediterranean Sea, when tropical species are detected it is difficult to establish the biogeographical origin of the invaders. Permanent studies in key areas, including the Strait of Gibraltar, the Bosphorus–Dardanelles Straits and the surrounding waters of the Suez Canal, will be useful for monitoring the expansion of tropical species.

Exclusively Mediterranean species

Endemism, the number of species living exclusively in the Mediterranean, is expected to be high in this semi-enclosed basin (Bianchi & Morri, 2000). The semi-enclosed Mediterranean conditions are thought to have led to speciation and neoendemism of Pliocenic invaders introduced during or after the Messinian salinity crisis (Furnestin, 1979). Relics of the Tethys Sea could survive the Messinian salinity crisis, as proposed for some benthic fauna (Wilke, 2003). Around 25% of the marine macroscopic species in the Mediterranean Sea are endemic (Bianchi & Morri, 2000), with > 50% endemism for some benthic fauna (Fredj *et al.*, 1992). In contrast to this general trend, Bouchet & Taviani (1992) reported that the deep fauna of the Mediterranean is characterized by a very low degree of endemism compared with the other areas of the world's oceans.

Table 2 Mediterranean–Indo-Pacific species according to Halim (1990, p. 16) and citations of these taxa from the Atlantic Ocean

Species	Records in Atlantic Ocean/comments
Ceratium egyptiacum Halim	= ? *Ceratium pulchellum* Schröder, see text
Dinophysis giganteum Kofoid *et* Michener	Closely related to *Dinophysis cuneus* (Schütt) Abé
Dinophysis umbosa Schiller	Wood (1968)
Heterodinium dubium Rampi	Reported only by the authority in the Pacific Ocean (Rampi, 1950)
Heterodinium minutum Rampi (?)	Non-existent, *Heterodinium minutum* Kofoid & Michener?
Histioneis inclinata Kofoid *et* Michener	Wood (1968), Balech (1988)
Histioneis longicollis Kofoid	Wood (1968), Dodge (1995)
Histioneis subcarinata Rampi	Balech (1971), only by Rampi (1950) in the Pacific
Gonyaulax ovalis Schiller	Doubtful taxa, insufficient description
Oxytoxum caudatum Schiller	Wood (1968), Marshall (1976), Moita & Vilarinho (1999), etc.
Oxytoxum laticeps Schiller	Wood (1968), Marshall (1976), Parke & Dodge (1976), Moita & Vilarinho (1999)
Oxytoxum variabile Schiller	Establier & Margalef (1964), Wood (1968), Margalef (1973), Marshall (1976), Parke & Dodge (1976), etc.
Prorocentrum maximum Matzenauer	Doubtful taxon, *Prorocentrum maximum* (Gourret) Schiller?
Protoperidinium hirobis Abé	Wood (1968), Balech (1971), Marshall (1976), Okolodkov (1998)
Protoperidinium nipponicum Abé	Steidinger *et al.* (1967), Lessard & Swift (1986), similar to *Protoperidinium ovum* Schiller
Protoperidinium tregouboffii Halim	See text
Pyrodinium schilleri (Matzenauer) Schiller	Only by Halim (1969) in the Mediterranean Sea

In the present study 48 dinoflagellate species were described and reported exclusively from the Mediterranean Sea, mainly by Rampi and Schiller in the Ligurian and Adriatic Seas, respectively (Table 3). Half these species were reported by a single author. Among the Dinophysiales Lindemann, species of the genera *Amphisolenia* Stein and *Histioneis* were poorly described and strongly resembled cosmopolitan species. In the original descriptions, based on single or few specimens, the authors failed to take into account the high morphological variability in the life cycle of Dinophysiales (Reguera & González Gil, 2001). As an example, Halim (1960) described several new species of *Histioneis* that strongly resemble immature (or damaged) specimens of a population of the cosmopolitan *Histioneis longicollis* Kofoid existing in the type locality (Fig. 2). *Ceratium brunellii* Rampi strongly resembles the cosmopolitan *Ceratium incisum* (Karsten) Jørgensen. Dodge & Saunders (1985) considered many of the species of *Oxytoxum* Stein, described by Rampi, as synonyms of common species. As occurred with other Noctilucales (Gómez & Furuya, 2004, 2005), *Cachonodinium* Kofoid goes unnoticed in the world's oceans and probably *Greuetodinium* (Greuet) Loeblich III is not a dinoflagellate.

Records of the remaining half of the exclusively Mediterranean species were reported by multiple authors, and thus are somewhat more credible. The identifications, however, were frequently based on older texts, which are imperfect. For example, Schiller (1933) described numerous unarmoured dinoflagellates of the genera *Amphidinium* Claparède & Lachmann and *Gymnodinium* Stein. These early descriptions were insufficiently detailed, often based on specimens deformed by the fixation used, and should be interpreted with caution (Fig. 3). More recently, Sournia (1986) questioned the validity of taxa such as *Archaeosphaerodiniopsis* Rampi, *Adinimonas* Schiller or *Pachydinium* Pavillard. While the contributions of Schiller and other earlier workers in the field are important references for dinoflagellate identification, researchers who rely solely on the older literature, without considering more recent work in the field of phytoplankton taxonomy, risk inaccuracies in their species accounts.

In the case of two genera, *Protoperidinium* Bergh and *Scrippsiella* Balech, identification at species level is limited to a few experts, which may explain the scarcity of records outside the Mediterranean Basin. The complex life cycle of the genus *Pyrocystis* Murray *ex* Haeckel precludes the consideration of *Pyrocystis margalefii* Léger for biogeographical purposes. The poor description of *Asterodinium libanum* Abboud-Abi Saab, the high morphological variability and the unknown life cycle of the order Brachidiniales Sournia, probably morphotypes of some species of *Karenia* G. Hansen & Moestrup, also prevent consideration of this taxon as an exclusively Mediterranean species (Gómez, 2003c; Gómez *et al.*, 2005).

These questionable dinoflagellate records reported as exclusively Mediterranean represented less than 7% of the total species. These taxa should be considered as 'false endemics' due to dubious taxonomic identification or the sparse geographical information. Based on the present study,

Table 3 Dinoflagellate species known exclusively from the Mediterranean Sea

Adinimonas oviforme Schiller
Alexandrium foedum Balech (Tyr)
**Amphisolenia sigma* Halim (Lev)
Amphidinium conus Schiller (Adr,Lig)
Amphidinium stigmatum Schiller (Lig,Ion,Adr)
**Archaeosphaerodiniopsis verrucosa* Rampi (Lig)
Asterodinium libanum Abboud-Abi Saab (Lig,Lev)
Cladopyxis quadrispina Pavillard
Dinophysis alata Jörgensen
**Cachonodinium caudatum* (Cachon *et* Cachon) Loeblich III (Lig)
**Ceratium brunellii* Rampi (Lig)
**Gonyaulax trottii* Rampi (Lig)
**Greuetodinium cylindricum* (Greuet) Loeblich III (Lig)
Gonyaulax elegans Rampi (Lig, also in BS)
Gymnodinium caput Schiller
Gymnodinium najadeum Schiller (also in BS)
Gymnodinium neapolitanum Schiller (also in BS)
Gymnodinium pulchrum Schiller (Lig,Adr)
Gymnodinium tridentatum Schiller (Adr)
Gymnodinium voukii Schiller
**Heterodinium balechii* Rampi (Lig)
**Heterodinium debeauxii* Rampi (Lig)
**Heterodinium grahamii* Rampi (Lig)
Heterodinium kofoidii Pavillard
**Heterodinium laticeps* Léger (Lig)
**Histioneis alata* Rampi (Lig)
**Histioneis bernhardii* Rampi (Lig)
**Histioneis elegans* Halim (Lig)
Histioneis expansa Rampi (Lig,Lev)
**Histioneis imbricata* Halim (Lig)
Histioneis faouzii Halim (Lig)
Histioneis kofoidii Forti & Issel (Tyr,Adr)
**Histioneis ligustica* Rampi (Lig)
Histioneis marchesonii Rampi (Bal,Lig,Lev)
**Histioneis rampii* Halim (Lig)
**Histioneis speciosa* Rampi (Lig)
**Histioneis sublongicollis* Halim (Lig)
**Histioneis villafranca* Halim (Lig)
**Oxytoxum obesum* Rampi (Lig)
Oxytoxum depressum Schiller
**Oxytoxum radiosum* Rampi (Lig)
Pachydinium mediterraneum Pavillard
**Parahistioneis sphaeroidea* Rampi (Lig)
**Prorocentrum venetum* Tolomio & Cavolo (Adr)
Protoperidinium maranense Tolomio (Adr)
P. parthenopes Zingone & Montresor (Tyr)
**Pyrocystis margalefii* Léger (Lig)
Scrippsiella ramonii Montresor (Tyr,Ion)

*Taxa reported only by the authority.

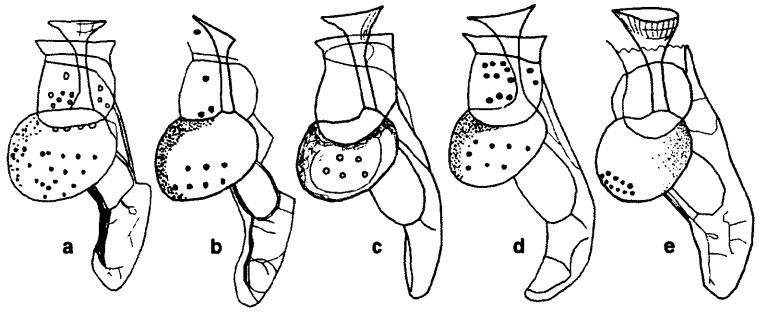

Figure 2 Illustrations of (a) *Histioneis villafranca* Halim; (b) *Histioneis elegans* Halim; (c) *Histioneis longicollis* Kofoid; (d) *Histioneis sublongicollis* Halim; (e) *Histioneis faouzii* Halim, adapted from Halim (1960). The new species described by Halim (1960) from single or few specimens strongly resemble the cosmopolitan *H. longicollis*. Scale bar = 20 μm.

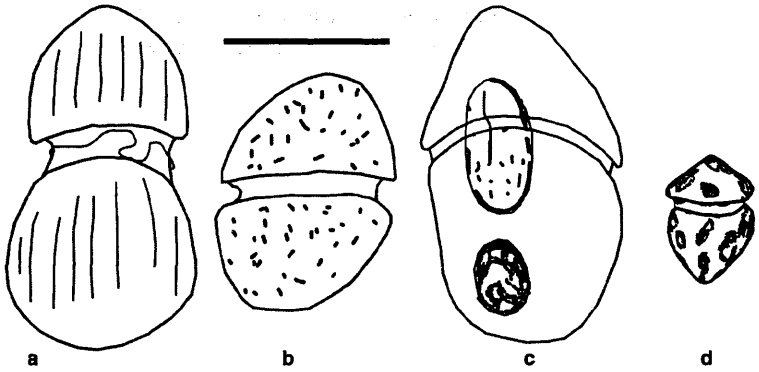

Figure 3 Illustrations of (a) *Gymnodinium caput* Schiller; (b) *Gymnodinium najadeum* Schiller; (c) *Gymnodinium neapolitanum* Schiller; (d) *Gymnodinium pulchrum* Schiller, adapted from Schiller (1933). The descriptions by Schiller (1933) are insufficiently detailed for precise identification of unarmoured taxa. Scale bar = 20 μm.

dinoflagellates show a lower percentage of endemic species compared with macroscopic or benthic species (Fredj *et al.*, 1992; Bianchi & Morri, 2000). In fact, no taxon considered in this study can be confirmed as being of exclusively Mediterranean origin. The Black Sea is an extreme case of a quasi-enclosed basin, which first came into contact with the world's oceans through the Bosphorus–Dardanelles Strait *c.* 12,000 yr BP (Çağatay *et al.*, 2000). Gómez & Boicenco (2004) compiled the dinoflagellate taxa cited in the Black Sea. They, likewise, concluded that no taxon could be recognized as endemic.

Neoendemism

According to van der Spoel (1994), the continuity of the marine pelagic environment provides very limited scope for isolation creating different habitats. Endemicity is difficult to prove in microscopic organisms because they are not easily recognizable: distinctive morphological features are rare compared with higher plants and animals; and the field has been distinctly understudied. Based on new molecular tools, the genetic distances in several ribosomal genes (18S rRNA for deep evolutionary divergences) are used to delimit the species. When physical barriers separate populations, as in the semi-enclosed Mediterranean Sea, the geographical isolation is expected to develop the endemism associated with genetic divergence.

If it is assumed that no species survived the extreme environmental changes that occurred during the Messinian salinity crisis and the rapid re-inundation that followed, the neoendemic taxa that entered through the Strait of Gibraltar from the Atlantic Ocean had a maximum of 5.33 Ma to diverge in gene sequence from their Atlantic ancestors. The molecular clock approach has been applied recently to marine dinoflagellates for the first time. John *et al.* (2003) estimated 23 Ma as the average time of origin of the *Alexandrium tamarense* species complex. Estimations based on the molecular clock approach should be considered very cautiously due to the difficulties in obtaining exact and comparable molecular clock rates for the non-protein-coding 16S gene, and other factors (Ayala, 1997). Nonetheless, according to the value reported by John *et al.* (2003), the 5.33 Ma after the re-inundation of Mediterranean Basin was insufficient for the speciation of dinoflagellates such as *Alexandrium* Halim.

Hydrographic circulation through the Strait of Gibraltar, with a strong surface inflow of Atlantic water, favours the introduction of Atlantic species (Gómez *et al.*, 2000). The Atlantic waters with a residence time of 80–100 years in the Mediterranean Basin could facilitate continuous exchange of plankton of Atlantic origin. This mechanism is more limited for non-free-swimming macroscopic or benthic species. This could explain the near absence of endemic dinoflagellate species in the Mediterranean compared with macroscopic organisms. The classic taxonomy based on morphological characters is insufficient for detecting morphologically similar, but distinct, forms in the Mediterranean Sea. Consequently, the occurrence of cryptic species cannot be discounted. The application of recent molecular techniques to the biogeography of the Mediterranean phytoplankton would contribute greatly to the clarification of these aspects of phytoplankton taxonomy.

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BIOSKETCH

Fernando Gómez has dedicated his research career to unravelling phytoplankton diversity and community structure in the Mediterranean Sea, particularly the Straits of Gibraltar and Ligurian Sea, the Eastern Atlantic, and the Northern, Equatorial and Southern Pacific. His favourite research topic is the taxonomy, ecology and biogeography of marine dinoflagellates. He is currently with the Protista & Mathematics Division of the Department of Zoology, Natural History Museum, London, UK, where he is investigating the morphological and molecular diversity of marine microplankton in European waters, with financial support from the European Commission's Marie Curie Intra-European Fellowship Scheme.

Editor: John Lambshead

3.2. Taxonomía y distribución de dinoflagelados poco conocidos:

3.2.1. *Brachidinium, Asterodinium, Microceratium.*

Gómez, F. 2003. New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae). *Nova Hedwigia* 77, 331-340.

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Gómez, F. 2007. Observations on a distinctive H-shaped dinoflagellate. An example of the projection of body extensions in gymnodinioid cells. *Acta Botanica Croatica* 66, aceptado.

Nova Hedwigia 77 3—4 331—340 Stuttgart, November 2003

New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae)

by

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With 22 figures and 1 table

Gómez, F. (2003): New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae). Nova Hedwigia 77: 331-340.

Abstract: New records of species of the rare planktonic dinoflagellate genus *Asterodinium* Sournia are reported. From the Mediterranean Sea and NE Atlantic Ocean: (1) three specimens of *Asterodinium* sp. sensu Sournia from the Gulf of Cádiz and Strait of Gibraltar (NE Atlantic Ocean), (2) one specimen of *Asterodinium* sp.1 from the Strait of Gibraltar, (3) three specimens of *Asterodinium* cf. *libanum* Abboud-Abi Saab from the Bay of Villefranche-sur-Mer(Ligurian Sea, NW Mediterranean Sea), (4) three specimens of *Asterodinium gracile* from the Tyrrhenian Sea and Strait of Sicily (Mediterranean Sea). Most taxa were recorded from 70 to 100 m depth, with exceptions in the Strait of Gibraltar and the Corsica Channel. From a longitudinal transect (138°E) in the Philippine Sea (NW Pacific Ocean) are reported: (5) four specimens of *Asterodinium gracile*, (6) *Asterodinium* cf. *gracile*, (7) one specimen of *Asterodinium* sp.1 and (8) *Asterodinium* sp.2. These records were collected between 50 to 175 m depths. *Asterodinium gracile* shows high morphological variation. The ecology of the genus is reviewed and discussed.

Key words: *Asterodinium*, dinoflagellate, Dinophyceae, Dinophyta, phytoplankton, Gulf of Cadiz, Strait of Gibraltar, Mediterranean Sea, Atlantic Ocean, Pacific Ocean, Kuroshio Current

Introduction

Asterodinium Sournia is a genus of photosynthetic planktonic marine dinoflagellates scarcely reported in the literature. These unarmored species are members of the family Brachidiniaceae* of the order Brachidiniales* A.R. Loeblich III ex Sournia (Loeblich III 1982, Sournia 1984) or Ptychodiscales Fensome, Taylor, Norris, Sarjeant, Wharton et Williams (Fensome et al. 1993).

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Species of the genus *Asterodinium* have dorsoventrally flattened cells with two elongate extensions radiating from the hyposoma and three from the episoma; a well-developed nucleus and chloroplasts are present. The genus was originally described from the Mozambique Channel (SW Indian Ocean) based on *Asterodinium gracile* Sournia (type species), *Asterodinium spinosum* Sournia and an undescribed species, *Asterodinium* sp. (Sournia 1972a,b). According to Sournia (1986, p. 50) no further records of these species exist. However, Estrada (1979) reported an unidentified species of *Asterodinium* in coastal waters of the NW Mediterranean Sea and Abboud-Abi Saab (1985) found *Asterodinium gracile* in Lebanese coastal waters (Eastern Mediterranean Sea). Abboud-Abi Saab (1989) further reported the new species, *Asterodinium libanum* Abboud-Abi Saab, but with an insufficient description. To the best of my knowledge, no other documented records of species belonging to the genus *Asterodinium* have been published.

This study reports the findings of several species of *Asterodinium* collected from 1997 to 2002 in the Mediterranean Sea, Eastern Atlantic and Western Pacific Oceans and provides information on the ecology and distribution of these species.

Material and methods

New records of *Asterodinium* from Mediterranean-Atlantic waters were obtained from samples collected during the following research cruises or coastal monitoring (Fig. 1): (1) Cruise carried out 18-25 June 1997 aboard R/V "Cornide" in the Gulf of Cádiz, Strait of Gibraltar and Alborán Sea (see García et al. 2002 for sampling details); (2) cruise carried out 2-9 September 1997 aboard R/V "Thalassa" in the Strait of Gibraltar (see Gómez et al. 2000 for sampling details); (3) coastal monitoring performed at the permanent station "Point B" (80 m depth) in the Bay of Villefranche-sur-Mer (Ligurian Sea) from January 1998 to January 2000 (see Gómez & Gorsky 2003 for sampling details) and (4) PROSOPE-cruise carried out 11-30 September 1999 aboard R/V "Thalassa" in the Eastern Atlantic Ocean and Mediterranean Sea (see Dolan et al. 2002 for sampling details).

Seawater samples were collected with oceanographic bottles, preserved with acidified Lugol's solution (e.g., Hasle & Syvertsen 1997, p. 334) and stored in the dark. Only during the cruise in the Strait of Gibraltar, seawater samples were concentrated using a 5-µm pore mesh. Sub-samples (10-100 ml) were allowed to settle for 24-48 h in Utermöhl chambers (Utermöhl 1958). Cells were observed with an inverted light microscope using bright field optics.

New records of *Asterodinium* from the Pacific Ocean were obtained from samples collected during a cruise aboard R/V "Soyo-Maru" in the Philippine Sea (Fig. 2). Seawater samples were collected with Niskin bottles from 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 125, 150, 175 and 200 m depth

(*) The family Brachidiniaceae and the order Brachidiniales are based on *Brachidinium* F.J.R. Taylor. In the original publication of Taylor (1963) this genus was spelt *Brachydinium*, but in 1967 Taylor introduced the orthographically corrected spelling *Brachidinium* [see also Articles 60 and 61 of the current version of the International Code of Botanical Nomenclature (ICBN; Greuter et al. 2000) dealing with the correction of orthographical errors]. Contrary to Sournia's (1973) conclusion, Taylor's (1967) correction of his own orthographical error is in no way contrary to these articles and should be followed. The spelling *Brachidinium* is indicated as the correct one in the ING (Farr et al. 1979) and in NCU-3 (Greuter et al. 1993); both entries are authored by Paul C. Silva, one of the most reliable specialists in the application of the ICBN to phycological nomenclature.

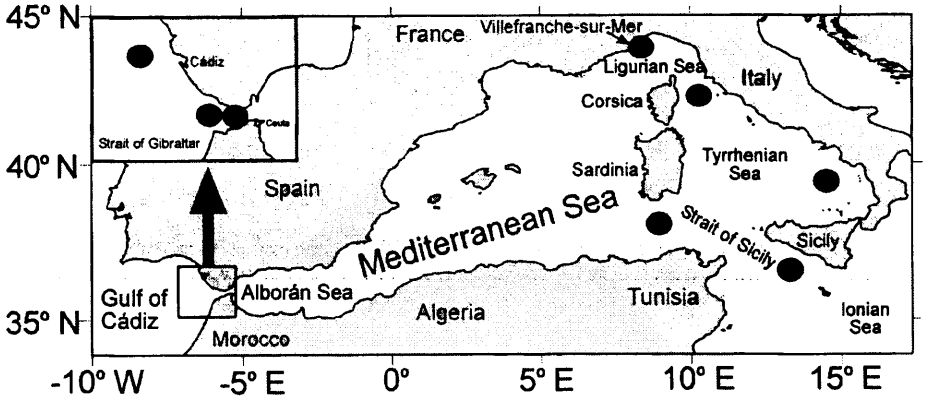


Fig. 1. Map of the Western Mediterranean Sea and Gulf of Cádiz.

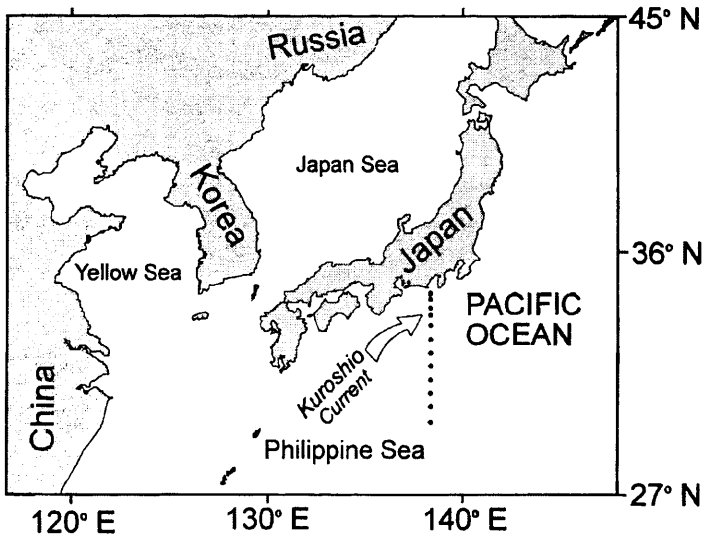


Fig. 2. Map of the NW Pacific Ocean.

along the meridian 138° from 28° 0N to 34° 20N. Nine stations were sampled from 3-20 May 2002 and nine from 3-9 July 2002. Samples were preserved with acidified Lugol's solution and stored at about 5°C. Samples were pre-concentrated by settling in glass cylinders, and concentrates were left to settle in standard sedimentation chambers. Concentrates equivalent to 400 ml were examined in a Nikon inverted microscope using bright field optics. Cells were photographed on an inverted light microscope connected to a Nikon digital camera.

Results

Asterodinium gracile Sournia

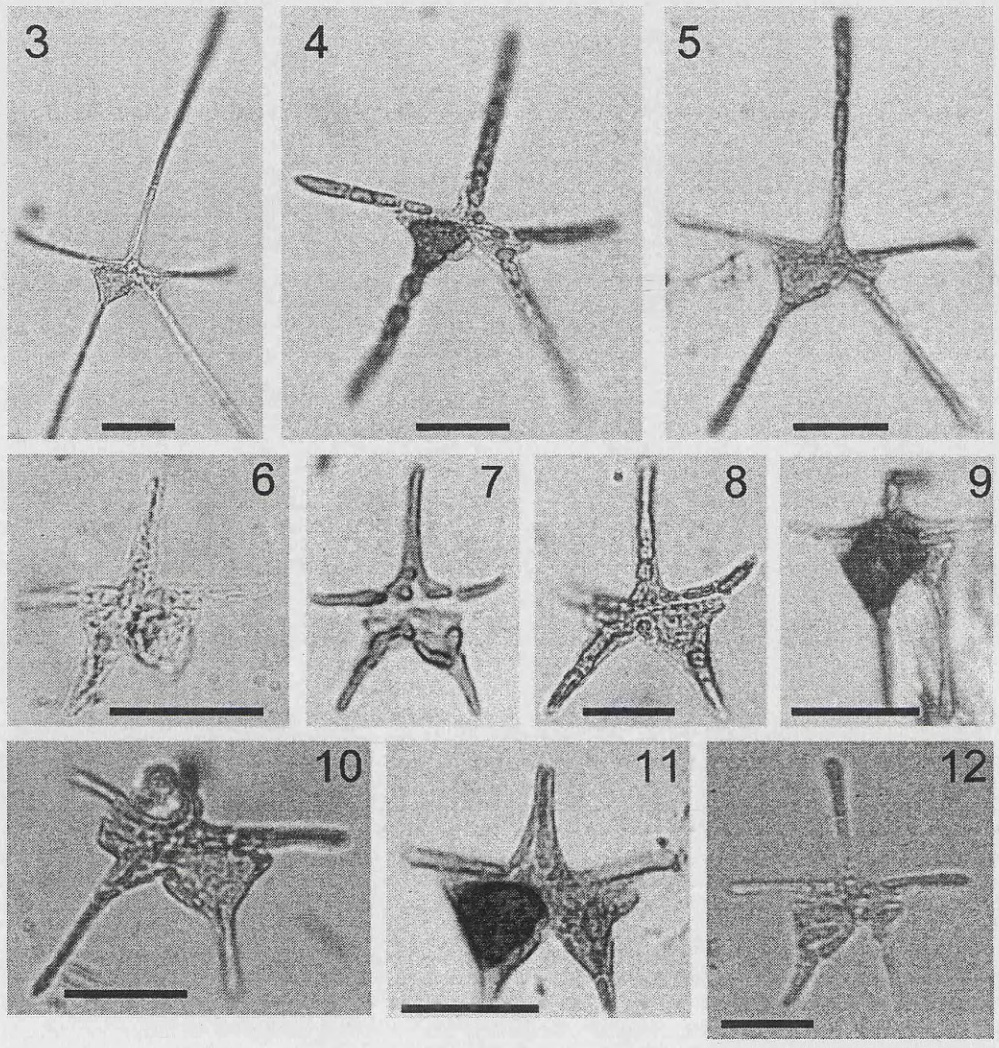
The identification is based on the drawing of *A. gracile* provided by Sournia (1972a). It is reproduced in Sournia (1986, p. 155) and in Fensome et al. (1993, p. 56) although erroneously named *Asterodinium spinosum*. To my best knowledge this is the only illustration available. In this study, it is assumed that *A. gracile* presents a high morphological variability in size and in the relative proportion of the extensions. As the extensions are flexible (especially the two lateral apical ones) the angle of the extensions with respect to the cell body is not considered as a taxonomic character. The distribution or number of chloroplasts did not seem to be usable for species differentiation.

In the Mediterranean Sea, four individuals were recorded in samples from the Tyrrhenian Sea and the Strait of Sicily collected during the PROSOPE-cruise (Fig. 1). Their maximal length was 49-52 µm and the width at the cingulum level was 21-23 µm (Figs 12, 22). All the specimens resembled *A. gracile* in shape. The lateral anterior extensions had rounded ends in all these specimens, whereas those illustrated by Sournia (1972a) had more pointed tips. Sournia's specimen of *A. gracile* had a maximum size of ~80 µm (as measured from the scale in his figure 8), thus being somewhat larger than the specimens collected in the Mediterranean Sea.

In the Pacific Ocean, 4 specimens more similar to the type material were collected from two stations located in the Kuroshio Current. At one station two specimens were collected at different depths (80 and 175 m). The specimen from 175 m depth (maximal length 90 µm, cingulum 28 µm, Figs 4, 14) was more intensely pigmented than the other one (maximal length 85 µm, cingulum 22 µm) (Figs 5, 15).

At a nearby station, two similar specimens were observed in the same sample. They showed more elongate appendices than all the other specimens (Figs 3, 13). Only one cell was measured, showing a maximal length of 160 µm, while the width of cell at the cingulum was 21 µm. The ratio between the length of the central apical extension and the cell width at the cingulum is approx. 1.3 in Sournia's (1972a) illustration. The specimen in my Figure 3 had a ratio >4, while the other specimens from the Pacific Ocean had a variable ratio ranging from 1.6-2.3. The specimens from the Mediterranean Sea also showed a ratio lower than the type material. For the present, all the cells are considered to be members of the *Asterodinium gracile* complex.

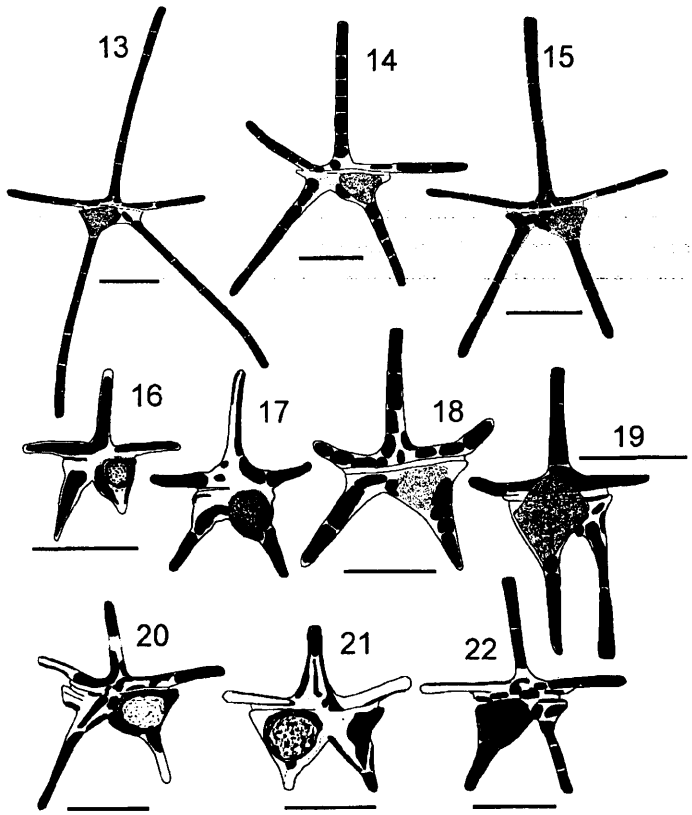
Another specimen is included in this group but here named *A.* cf. *gracile* (Figs 10, 20). It was found in offshore subtropical waters of the Philippine Sea. It differed from the specimens of the *A. gracile* complex by its shorter extensions. The width of the cell at the level of the cingulum was 27 µm. The distance between the tips of the two lateral apical arms was 52 µm and the length of the longer antapical extension was 30 µm. No precise measurement of the total length was taken due to the bending of the central apical extension, but it seems to be around ~55 µm (Figs 10, 20).



Figs 3-12. Photomicrographs of *Asterodinium* spp. Figs 3-5. *Asterodinium gracile* from the Pacific Ocean. Fig. 6. *Asterodinium* sp. sensu Sournia (1972a) from the Gulf of Cádiz. Fig. 7. *Asterodinium* sp.1 from the Strait of Gibraltar. Fig. 8. *Asterodinium* sp.1 from the Pacific Ocean. Fig. 9. *Asterodinium* sp.2 from the Pacific Ocean. Fig. 10. *Asterodinium* cf. *gracile* from the Pacific Ocean. Fig. 11. *Asterodinium* cf. *libanum* from the Mediterranean Sea. Fig. 12. *Asterodinium gracile* from the Mediterranean Sea. Scale bars 20 mm.

Asterodinium cf. **libanum** Abboud-Abi Saab

In samples collected in the Bay of Villefranche-sur-Mer (Ligurian Sea), three individuals were observed. The length was 42 µm and the cingulum was 27 µm long. This taxon is morphologically different with a less delicate appearance compared to other species of *Asterodinium* with short extensions (Figs 11, 21). It is here called *A.*



Figs 13-22. Line drawings of *Asterodinium* spp. Figs 13-15. *Asterodinium gracile* from the Pacific Ocean. Fig. 16. *Asterodinium* sp. sensu Sournia (1972a) from the Gulf of Cadiz. Fig. 17. *Asterodinium* sp.1 from the Strait of Gibraltar. Fig. 18. *Asterodinium* sp.1 from the Pacific Ocean. Fig. 19. *Asterodinium* sp.2 from the Pacific Ocean. Fig. 20. *Asterodinium* cf. *gracile* from the Pacific Ocean. Fig. 21. *Asterodinium* cf. *libanum* from the Mediterranean Sea. Fig. 22. *Asterodinium gracile* from the Mediterranean Sea. Scale bars 20 mm.

libanum, although Abboud-Abi Saab (1989) did not provide a Latin diagnosis and neither line drawings nor good quality illustrations; therefore it is difficult to compare with the original description.

Asterodinium sp. sensu Sournia (1972a)

Sournia (1972a) reported a single cell from the Indian Ocean, but he did not describe it as a new species because it was considered that the specimen was damaged.

Three specimens that strongly resemble *Asterodinium* sp. as reported by Sournia (1972a) in morphology and size were collected from the Eastern Atlantic Ocean. The first specimen was found in the Gulf of Cádiz (Figs 6, 16). Two similar specimens

Table 1. New records of *Asterodinium*.

Taxa	#	Location	Lat N	Long	depth	Date	Figure
Asterodinium gracile Sournia	1	Sardinia Channel	37° 59	8° 32 E	90	17/09/1999	
A. gracile Sournia	1	Strait of Sicily	36° 28	13° 19 E	80	18/09/1999	
A. gracile Sournia	1	South Tyrrhenian Sea	39° 12	14° 08 E	70	27/09/1999	12
A. gracile Sournia	1	Corsica Channel	41° 54	10° 26 E	30	28/09/1999	
A. cf. *gracile* Sournia	1	Offshore Philippine Sea	32° 00	138° E	90	13/05/2002	10
A. gracile Sournia	1	Kuroshio area	33° 00	138° E	80	07/07/2002	5
A. gracile Sournia	1	Kuroshio area	33° 00	138° E	175	07/07/2002	4
A. gracile Sournia	2	Kuroshio area	33° 30	138° E	100	07/07/2002	3
Asterodinium cf. *libanum* Abboud-Abi Saab	1	Villefranche Bay	43° 41	7° 19 E	50	Sept98	
A. cf. *libanum* Abboud-Abi Saab	2	Villefranche Bay	43° 41	7° 19 E	50	Sept-Oct99	11
Asterodinium sp. sensu Sournia 1972	1	Gulf of Cádiz	36° 34	6° 47 W	75	23/06/1997	6
A. sp. sensu Sournia 1972	2	Strait of Gibraltar	35° 54	5° 38 W	20	5/09/1997	
Asterodinium sp.1	1	Strait of Gibraltar	35° 58	5° 55 W	100	3/09/1997	7
Asterodinium sp.1	1	Kuroshio area	33° 00	138° E	50	11/05/2002	8
Asterodinium sp.2	1	Kuroshio area	31° 00	138° E	125	06/07/2002	9

were subsequently collected in the Strait of Gibraltar (Fig. 1, Table 1). The maximal length was 32-34 μm and the cell width at the cingulum was 14 μm. Also, the specimens collected from the Gulf of Cádiz and Strait of Gibraltar presented a 'damaged aspect', whereas other cells in the plankton appeared undamaged.

Asterodinium sp.1

This taxon differs from previous records by the presence of shorter extensions with rounded tips and with a cell body slightly more elongated than in *A.* cf. *libanum*. One specimen was collected at the Atlantic side of the Strait of Gibraltar (Figs 7, 17) (Unfortunately no size measurements were performed). A second specimen, apparently similar to the Atlantic one, was collected from the offshore subtropical waters of the Philippine Sea (Figs 8, 18). The maximal length was 51 μm and the width at the cingulum was 27 μm.

Asterodinium sp.2

From the waters of the Kuroshio Current was collected a specimen that differed from other records. Cells possessed two parallel antapical extensions, short lateral apical extensions, and a longer central apical extension (Figs 9, 19). The nucleus occupied a higher proportion of the cell body than in the other species and extended into the episoma. Due to the bending of the central apical extension, the maximum length is estimated to be around ~60 μm. The width of the cell at the cingulum was 18 μm.

Discussion

Ecological characteristics

Due to the small number of observations, it is difficult to establish the ecological characteristics of *Asterodinium*. However some trends were noticed in the vertical distribution of the taxa (Table 1).

In the Indian Ocean, Sournia (1972a,b) recorded individuals of *Asterodinium* at 100 m depth. Estrada (1979) reported an unidentified species of *Asterodinium* from surface waters of the NW Mediterranean Sea. In the Bay of Villefranche (Ligurian Sea), three specimens of *Asterodinium libanum* were collected at 50 m (at a station with a maximal depth of 80 m, see Gómez & Gorsky 2003). In the Tyrrhenian basin and the Sicily Strait, three specimens of *Asterodinium gracile* were collected in deep waters (70-90 m depth), and one individual at 30 m depth. On the Atlantic side of the Strait of Gibraltar, a specimen of *Asterodinium* sp.1 was found at 100 m depth, while in the Gulf of Cádiz, one specimen of *Asterodinium* sp. sensu Sournia (1972a) was found at 75 m depth. Concerning the records of *Asterodinium* sp. sensu Sournia (1972a) found near the sill of the Strait of Gibraltar, it should be taken into account that mixing events can alter the vertical distribution of the species (Gómez et al. 2000). *Asterodinium* species have well-defined chloroplasts and this may be an adaptation to the low irradiance levels in deep waters, since other photosynthetic deep waters species (e.g., *Ceratium platycorne* Daday) also contain higher concentrations of chlorophyll compared to taxa found in shallow water (Falkowski 1980). The most recent records clearly confirm this trend, one specimen collected at 175 m depth just below the Kuroshio axis (Fig. 4) presented a healthy aspect with more intense pigmentation compared to the shallower one (Fig. 5). It should be taken into account that the warm Kuroshio Current is characterized by highly transparent waters. Thus, the genus *Asterodinium* may be considered as a member of the shade flora (Sournia 1982).

Concerning the temporal distribution of *Asterodinium*, some trends are apparent:

Estrada (1979) reported an unidentified species of *Asterodinium* in September 1975 along the Mediterranean Spanish coasts. Abboud-Abi Saab (1985) from 3 years of monitoring in Lebanese coastal waters exclusively reported *Asterodinium gracile* in the autumn and *Asterodinium* sp. in the spring. During our biannual study of the phytoplankton composition of the Bay of Villefranche-sur-Mer, *Asterodinium* was observed only in September and October (Table 1). Since the research cruises were performed in June and September, the offshore records only appeared during these months. Late summer is the most oligotrophic period in the Mediterranean Sea and it seems to be the most favourable period for the development of these species. Gómez & Claustre (2003) mention that the recent occurrence of *Asterodinium* in the areas of the western Mediterranean Sea intensively investigated in the past (e.g., the Ligurian Sea; see Gómez 2003) could be associated with the progressive warming of the Mediterranean waters and unusual high temperatures in September 1999.

Due to the small size and delicate features such as pelliculate cells with flexible radiating arms, plankton net sampling probably damages specimens of *Asterodinium*. Their detection in oligotrophic waters requires sedimentation of large volumes of seawater with very low phytoplankton abundance. *Asterodinium* in not included in the most commonly used literature for phytoplankton identification, with the exception of Sournia (1986) and Fensome et al. (1993), and it is likely this it often escapes notice during routine analyses.

Further research should address the *Asterodinium gracile* complex; does it constitute one species with high morphological variability, depending on environmental conditions, or are different species involved?

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The genus *Asterodinium* (Dinophyceae) as a possible biological indicator of warming in the western Mediterranean Sea

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The presence of two dinoflagellate species of the genus *Asterodinium*, which are a priori representative of warm waters, is reported for the first time in the western Mediterranean Sea. *Asterodinium libanum* was identified in the Bay of Villefranche-sur-Mer (Ligurian Sea), while *Asterodinium gracile* is reported in the Tyrrhenian Sea. These findings are discussed in the context of the progressive warming of Mediterranean waters.

Since 1960, a monotonic increase of the temperature has been recorded in the Mediterranean waters, apparently as a result of the combined global warming and local anthropogenic effects (Béthoux et al., 1990; Turley, 1999). Several studies have shown that the marine biodiversity of the Ligurian and Tyrrhenian basins is sensitive to climate change, with tropical species appearing since 1985 (Francour et al., 1994; Astraldi et al., 1995). However most of the studies on changing biodiversity in the Mediterranean Sea, deal with macroscopic species such as fish, invertebrates or macroalgae (Bianchi & Morri, 2000).

During the last century, at least 16 exotic phytoplankton species have become common in European Atlantic waters (Elbrächter, 1999) with the establishment of thermophilic phytoplankton species in the North Sea (Nehring, 1998). However little is known about changes affecting the phytoplankton community of the Mediterranean Sea.

Asterodinium is a distinctive genus of unarmoured dinoflagellates; cells are dorsoventrally flattened, with two characteristic radiating elongate extensions from the hypotheca and three other arms from the epitheca; they present a well-developed nucleus and chloroplasts. The genus was initially reported from the tropical Indian ocean with the description of two species *Asterodinium gracile* and *A. spinosum* (Sournia, 1986). Later, *Asterodinium gracile* and the new species *A. libanum* were reported in Lebanese coastal waters (eastern Mediterranean Sea) (Abboud-Abi Saab, 1989).

The present study reports recent records of *Asterodinium* species in the western Mediterranean Sea and is suggested as possible biological indicator of warming.

Phytoplankton identification was performed as part of two studies. The first study was conducted over two years (1998–2000) at a permanent station (Station B) in the Bay of Villefranche-sur-Mer (Ligurian Sea, north-west Mediterranean Sea). The second study was performed as part of the PROSOPE cruise carried out in September 1999 aboard the RV 'Thalassa' from the Moroccan Atlantic coast to the eastern Mediterranean Sea (Figure 1). Unconcentrated seawater samples were preserved with Lugol's solution and kept in cold and dark conditions until analysis in the laboratory. Subsamples (50–100 ml) were allowed to settle for 24–48 h in Utermöhl chambers and observed by inverted light microscopy.

Three specimens of *Asterodinium libanum* Abboud-Abi Saab have been observed in the Bay of Villefranche-sur-Mer in September 1998 and September–October 1999 at 50 m depth. In September 1999, four individuals of *Asterodinium gracile* Sournia were recorded at four stations in the Tyrrhenian Basin and the Sicilian Strait, mostly in the 70–90 m layer (Figure 2).

The phytoplankton composition of the Ligurian Sea has been extensively investigated in the past. Halim (1960) reported the composition of dinoflagellates from a 3-y study (1952–1954) at the same Station B where we report the presence of *A. libanum* for the first time. The *Asterodinium* genus was described for the first time in 1972 but this genus is distinctive and easily identifiable, thus removing the possibility that Halim (1960) might have misidentified it. For example, Halim (1960) described six new species of *Histioneis*, a genus in the same size range as *Asterodinium* which is also preferentially found in the deep waters of the Bay of Villefranche.

The Tyrrhenian basin has also been intensively investigated, but most of the studies were performed in the Bay of Naples or coastal lagoons. These shallow and eutrophic environments seem to be unfavourable for the development of *Asterodinium* species.

Coinciding with the records of *A. gracile* in September 1999, a climatically-driven ecosystem disturbance was reported in the

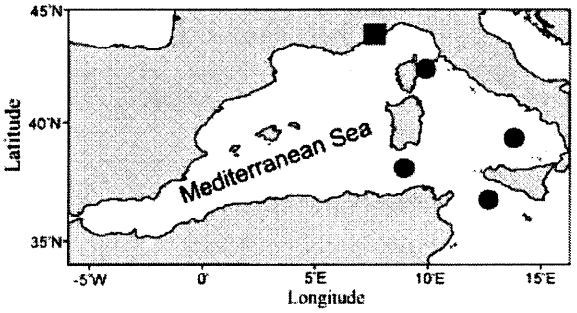

Figure 1. Location of the records of *Asterodinium* Sournia in the western Mediterranean Sea. ■, *A. libanum*; ●, *A. gracile*.

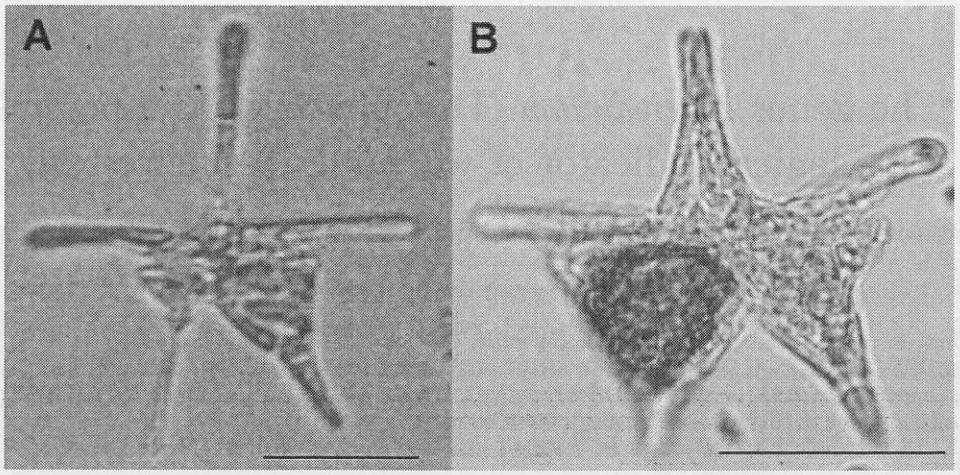

Figure 2. Light microscopy photographs: (A) *Asterodinium gracile* (×400) from the Tyrrhenian Sea; (B) *Asterodinium libanum* (×630) from the Bay of Villefranche-sur-Mer (Ligurian Sea). Scale bar: 20 μm.

north-western Mediterranean, with a deepening of the thermocline and an anomalous increase of summer sea surface temperatures (of 2–3°C); these changes resulted in marked mortality of sessile invertebrates (e.g. sponges and gorgonians) (Romano et al., 2000; Cerrano et al., 2000).

Seawater warming can affect the marine biota by a direct influence of temperature, causing changes in survival, reproductive success and dispersal pattern and an indirect influence due to the change of the ocean circulation patterns (Bianchi & Morri, 2000). Since the completion of the Suez Canal in 1869 and more recently with the reduction of salinity of Bitter Lakes, the introduction of tropical species directly through the Suez Canal or via ballast waters seems to be favoured (Halim, 1990). The progressive warming of the Mediterranean Sea, and possibly the 1999 thermal anomaly might have favoured the increase in abundance of warm-water species such as those of the *Asterodinium* genus.

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Morphology of *Brachidinium capitatum* F.J.R. Taylor (Brachidiniales, Dinophyceae) collected from the western Pacific Ocean

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Abstract — This is a first report of the genus *Brachidinium* F.J.R. Taylor from the Pacific Ocean. Of the 17 specimens of *B. capitatum* reported here, 12 were collected from the vicinity of the Kuroshio in May (2 specimens) and July (10 specimens), 3 from the western equatorial Pacific Ocean, one from the Sulu Sea, and one from Tanabe Bay, Japan. The last-mentioned specimen was observed live. For the first time, the flagella and the sulcus of a member of the order Brachidiniales A.R. Loeblich III ex Sournia are depicted in photomicrographs. The ventral view corresponds to that seen when the position of the nucleus is in the left side of the cell. In several specimens, DAPI-staining showed a secondary nucleus located in the opposite side of the dinokaryon nucleus. In the live specimen, the sulcus was visible and the lateral extensions were observed to be moveable.

***Brachidinium* / *Brachydinium* / binucleate dinoflagellate / Pacific Ocean / phytoplankton / taxonomy**

Résumé — Morphologie de *Brachidinium capitatum* F.J.R. Taylor (Brachidiniales, Dinophyceae) récolté à l'ouest de l'Océan Pacifique. C'est la première signalisation du genre *Brachidinium* F.J.R. Taylor dans l'Océan Pacifique. Parmi les 17 spécimens de *B. capitatum* rapportés ici, 12 ont été trouvés à proximité du Kuroshio en mai (2 spécimens) et juillet (10 spécimens), 3 dans l'Océan Pacifique équatorial occidental et enfin, un seul spécimen dans la mer de Sulu ainsi que dans la Baie de Tanabe, Japon. Le dernier spécimen a été observé vivant. Pour la première fois, les flagelles et le sulcus d'un membre de l'ordre des Brachidiniales A.R. Loeblich III ex Sournia sont illustrés par des photomicrographies. La vue ventrale correspond à ce que l'on voit quand le noyau est du côté gauche de la cellule. Dans plusieurs spécimens, l'utilisation de la coloration au DAPI a montré un noyau secondaire situé du le côté opposé au noyau dinokaryon. L'observation du spécimen vivant a montré nettement le sulcus ainsi que la motilité des prolongements latéraux.

***Brachidinium* / *Brachydinium* / dinoflagellé binucléé / Océan Pacifique / phytoplancton / taxonomie**

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INTRODUCTION

Brachidinium F.J.R. Taylor is a genus of photosynthetic planktonic marine unarmored dinoflagellates [usually misspelled as *Brachydinium*, see Gómez (2003a)]. *Brachidinium* and *Asterodinium* Sournia constitute the family Brachidiniaceae, placed in the order Brachidiniales A.R. Loeblich III *ex* Sournia (Loeblich III, 1982; Sournia, 1984), or Ptychodiscales Fensome, Taylor, Norris, Sarjeant, Wharton *et* Williams (Fensome *et al.*, 1993). According to Steidinger & Tangen (1997, p. 468) *Brachidinium* has flattened cells with four elongate extensions radiating from the hyposoma and an apical process on the episoma. The sulcus has not been observed, but an incomplete cingulum and chloroplasts are present. A large, ovoid nucleus occupies most of the cell body.

The type species *Brachidinium capitatum* F.J.R. Taylor (Taylor, 1963) and one other species, *Brachidinium catenatum* F.J.R. Taylor, have been described from the southwest Indian Ocean (Taylor, 1967; see Figs 2-4). The author mentioned that the latter species might be a small neritic or summer form of *B. capitatum* (Taylor, 1967) (Fig. 4). Sournia (1972) also reported *B. capitatum* (see Figs 5-6) and described two new taxa, *Brachidinium taylorii* Sournia (see Fig. 7) and *Brachidinium brevipes* Sournia (see Fig. 8), also from the southwest Indian Ocean. According to Sournia (1972, p. 153) *B. taylorii* shows a robust aspect with thicker arms than the type species and a shorter apical protuberance. The surface of the cell is covered with fine peaks "fines côtes ou crêtes". *Brachidinium brevipes* shows shorter arms, a very reduced central body and is also covered with fine peaks (Sournia, 1972, p. 153-4).

Subsequently, *B. capitatum* and *Brachidinium* sp. were reported from the southern waters of the Indian Ocean and the Arabian Sea, respectively (Sournia *et al.*, 1979; Tarran *et al.*, 1999). The type species was also reported from the northeast Atlantic Ocean (Margalef, 1973) and the Mediterranean Sea (Léger, 1971; Abboud-Abi Saab, 1985; Viličić, 1998). In the northwest Mediterranean Sea, Estrada & Salat (1989) reported *Brachidinium* as a component of the deep phytoplankton assemblages and Palau *et al.* (1991) reported *Brachidinium* sp. from a cave. *Brachidinium taylorii* Sournia was reported from the southeast Atlantic Ocean (Kruger, 1979) and the Mediterranean Sea (Margalef, 1995). The latter author also listed *Brachidinium* "transversum" but with no illustrations or additional information (Margalef, 1995).

The morphology of the species of *Bachidinium* is poorly known due to a lack of records, detailed illustrations and information on the ultrastructure (i.e., flagellum/flagella; sulcus; nuclei; etc). Taylor (1963) did not observe the flagellum/flagella or cingulum and placed *Brachidinium* in the order Dinococcales Pascher. He proposed a tentative orientation for the genus (Figs 2-3). Taylor (1980, p. 67) showed a species of *Brachidinium*, which has a poorly defined sulcus, a "longitudinal flagellum" and the dinokaryon nucleus in the left side of the cell (Fig. 9). Fensome *et al.* (1993, p. 3) included a line drawing of *B. capitatum* with two flagella (Fig. 10). They did not mention flagella or sulcus in the family Brachidiniaceae (p. 56), but illustrated dorsal and ventral views of *B. capitatum,* in which the ventral view corresponds to the position of the dinokaryotic nucleus in the right side of the cell (Figs 5-6). Fensome *et al.* (1993, p. 56) reported that the orientation was based on Sournia (1972, 1986). However, Sournia (1972, 1986) included no illustration of flagellum/flagella or sulcus of *Brachidinium*. Sournia (1972) introduced a terminology describing the orientation of the order Brachidiniales and considered that the dinokaryotic nucleus is displaced to one side and

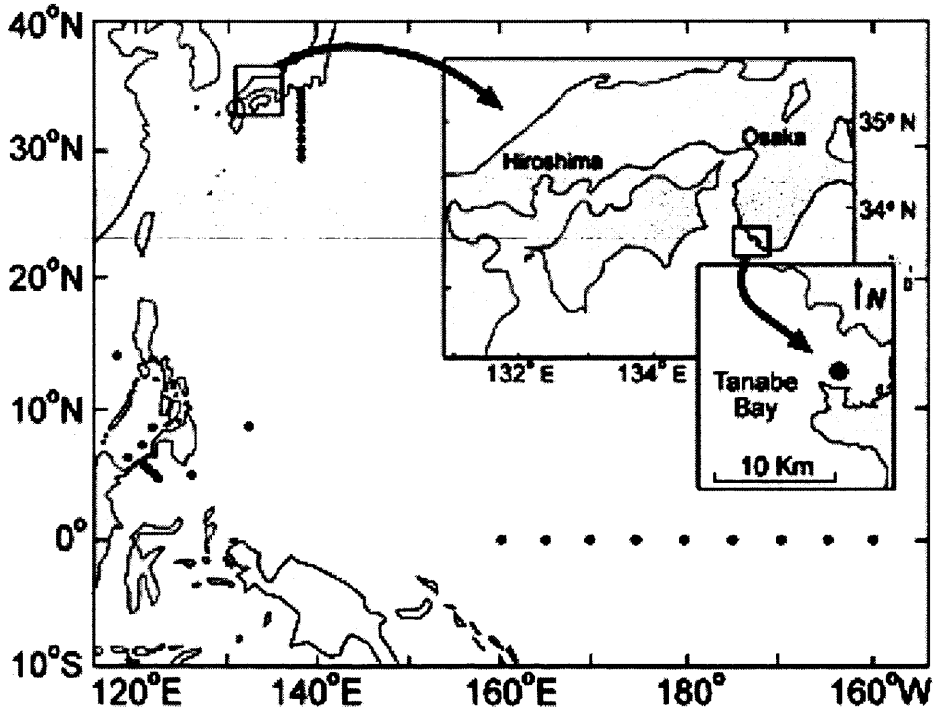
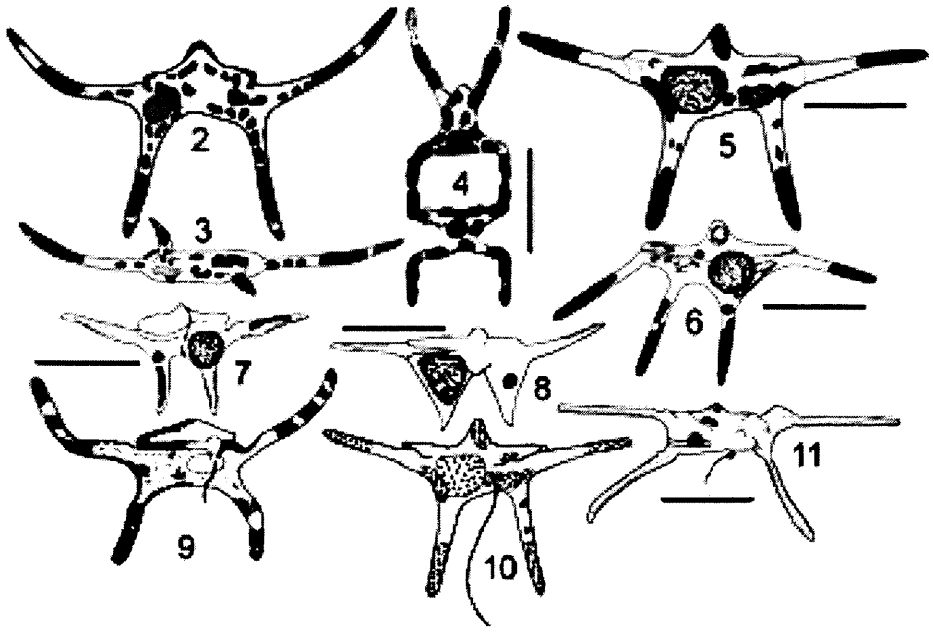


Fig. 1. Location of the sampling stations in the western Pacific Ocean. The inset shows the Tanabe Bay where a live specimen was collected.

the extensions or arms closer to the nucleus were the "left" extensions. Uncertainties remained, however, and Sournia (1986, p. 49) doubted whether the cells were dorso-ventrally or laterally flattened.

Sournia (1986, p. 50), based on the records by Léger (1971), reported that *Brachidinium* possesses at least one flagellum, but that the point of insertion remained unknown. Léger (1971) collected 30 specimens named as *B. capitatum*. However his figure, reproduced here (Fig. 11) does not seem to represent the type species. His specimen drawing has two extensions radiating from the hyposoma, and two extensions and a central process from the episoma. It is intermediate between *Asterodinium* and *Brachidinium*. Sournia (1972) commented on the possibility of an 'optical illusion' in the position of the cingulum. His specimen has the dinokaryotic nucleus in the left side and a hypothetical 'sulcal' flagellum arising from the rear and the nucleus in the right side of the cell (Fig. 11). Léger (1971) reported that he was unable to locate the insertion of the flagellum.

This study reports for the first time the flagella and the sulcus in *Brachidinium*, including photomicrographs on the moveable extensions of a live specimen, and the occurrence of a secondary nucleus (confirmed by DAPI staining).



Figs 2-11. Line drawings of several species of *Brachidinium* reported in the literature. Fig. 2. *B. capitatum* adapted from Taylor (1963). Fig. 3. Ventral view of *B. capitatum* according to Taylor (1963). Fig. 4. *Brachidinium catenatum* F.J.R. Taylor adapted from Taylor (1967). Figs 5-6. *B. capitatum* adapted from Sournia (1972). These figures were also reproduced by Fensome *et al.* (1993), who proposed that they represented ventral and dorsal views, respectively. Fig. 7. *Brachidinium taylorii* Sournia adapted from Sournia (1972). Fig. 8. *Brachidinium brevipes* Sournia adapted from Sournia (1972). Fig. 9. A ventral view of a member of the genus *Brachidinium* showing the longitudinal flagellum adapted from Taylor (1980, p. 67). Fig. 10. A ventral view of *B. capitatum* with two flagella adapted from Fensome *et al.* (1993, p. 3) apparently based on Sournia (1972, 1986). Fig. 11. "Brachidinium capitatum" adapted from Léger (1971). Scale bars 20 μm.

MATERIAL AND METHODS

Samples were collected during several cruises in the western Pacific Ocean: 1) Two cruises on board R/V *Soyo Maru* (13-20 May and 3-10 July 2002) along the meridian 138° in the vicinity of the Kuroshio Current. Nine stations were sampled from 30° 30' N to 34° 15' N in May, and 10 stations were sampled from 30° 0' N to 34° 20' N during the July cruise. At each station, 15 depths from 5-200 m were sampled with Niskin bottles; 2) on board R/V *Hakuho Maru* (7 November-18 December 2002) in the Celebes, Sulu and South China Seas. Samples were collected using Niskin bottles at 10 stations at six depths from 0 to 150 m depth; 3) aboard R/V *Mirai* (15-28 January 2003) along the equator from 160°E to 160°W (Fig. 1). Samples were collected with Niskin bottles from 9 stations at 14 depths between 0 to 200 m depth. During all the cruises, samples were preserved with acidified Lugol's solution (Hasle and Syvertsen 1997, p. 334) and stored at 5° C. Samples were pre-concentrated by settling in glass cylinders, and concentrates settled in standard sedimentation chambers. Concentrates equivalent

to 400 mL were observed with a Nikon inverted microscope equipped with a Nikon digital camera.

Several of the Lugol fixed specimens were isolated with a capillary from the chambers, transferred to a glass slide, and observed with an Olympus microscope equipped with Nomarski Differential Interference Contrast (D.I.C.) system. High magnification microphotographs (×600; ×1000) were obtained with an Olympus digital camera. Several specimens were stained by adding DAPI (4,6-diamidino-2-phenylindole). DAPI specifically binds to double stranded DNA, and when excited with U.V. light the DAPI-DNA complex fluoresces a bright blue (Porter & Feig, 1980). Epifluorescence microscopy was done with Olympus and Zeiss microscopes equipped with UV excitation facility.

In addition, one specimen collected from the coastal waters of Japan was observed live. Seawater samples were monthly collected from a station in Tanabe Bay (see inset in the Fig. 1) at 0,5, 10,15 m depths and one metre above the bottom (19.5 m depth). Samples (1 l) were filtered through an 8 mm pore size Millipore cellulose acetate filter at low pressure (<100 mmHg) to a final volume of 50 ml. This concentrate was left to settle in a composite chamber. From the bottom of the chamber, 1 ml was examined on a Sedgewick-Rafter counting chamber. The specimen was isolated with a capillary, transferred to a glass slide and cover with a glass slide. The specimen was observed and photographed with an Olympus light microscope and Olympus camera by using bright field.

RESULTS AND DISCUSSION

A total of 17 specimens of the genus *Brachidinium* were observed in the upper 90 m depth during the four cruises in the western Pacific Ocean (Fig. 1). Ten specimens were observed in the vicinity of the Kuroshio in July and only two in May. The maximum occurrence was in July (30° 0' N, 138° E at 60 m depth) with 3 specimens per sample (7.5 cells l^{-1}) (Tab. 1).

All the records are considered to be of the type species, *B. capitatum*, which, although from the same sample, showed some variation in size as well as the relative angle of the extensions with respect the cell body. The maximum length of the cells ranged from 50 to 140 mm and the width of the cell at the cingulum was 25-55 μm.

Cell orientation

Brachidinium is a flattened athecate dinoflagellate. The presence of long appendices, resulting in different inclinations of the cell, plus the cell transparency, make it difficult to observe ultrastructural details (such as the insertion of the flagella) by light microscopy.

The transverse flagellum (TF hereafter) was observed in several specimens by using D.I.C. optics. In one specimen, the TF was also observed under inverted microscopy when it was separated from the cingulum (Figs 12-14). The nucleus of this specimen was located in the right side of the cell. The TF was free moving, displaced from the cingulum groove in the rear (reverse) focus of the cell (Fig. 12) and turned to the front of the cell in the left extremity of the cingulum groove (Fig. 13). In the front of the cell the TF ran all along the cingulum and no insertion was observed (Fig. 14). Subsequently, the insertion of the flagellum was

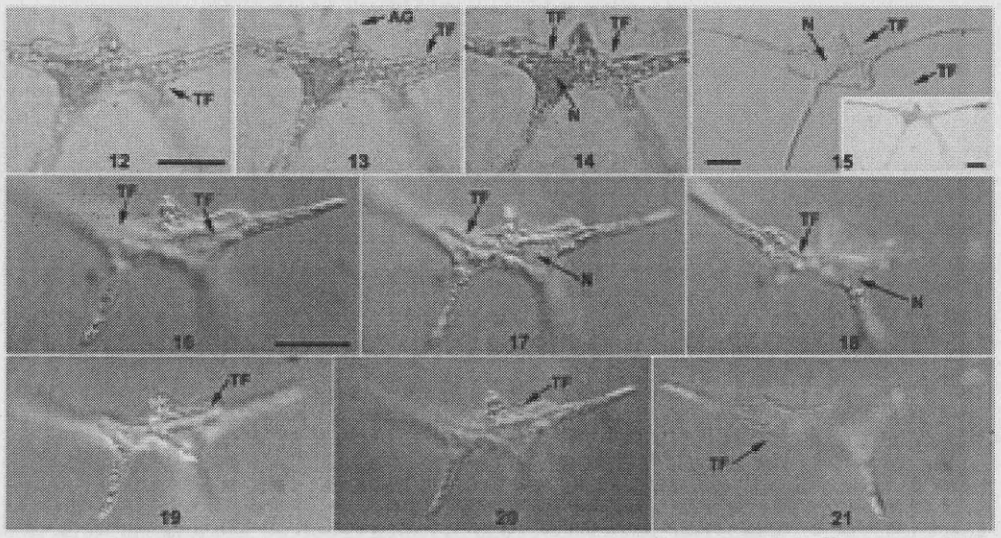
Table 1. Number of specimens recorded, date, stations, depth (m) in meters, geographic coordinates (latitude, longitude) and figures of the records of *Brachidinium* in the western Pacific Ocean.

#	*Date*	*Sta.*	*(m)*	*Lat N*	*Long*	*Figure*
1	24/1/1995	20	- 19.5	33° 42'	135° 21' E	Figs 27-28
1	10/5/2002	C3	- 5	33° 30'	138° E	
1	13/5/2002	C13	- 5	30° 30'	138° E	
2	7/7/2002	C8	- 20	33° 30'	138° E	Figs 16-21
1	7/7/2002	C7	- 50	33°	138° E	
1	7/7/2002	C6	- 5	32° 30'	138° E	
1	6/7/2002	C5	- 40	32°	138° E	
1	6/7/2002	C2	- 60	31° 30'	138° E	Fig. 26
1	4/7/2002	B1	- 10	30°	138° E	Figs 22-25
3	4/7/2002	B1	- 60	30°	138° E	
1	3/12/2002	10	- 30	8° 50'	121° 48'E	
1	15/1/2003	6	- 1	0°	160° E	
1	17/1/2003	7	- 90	0°	165° E	Figs 12-15
1	25/1/2003	13	- 80	0°	165° W	

located in the rear focus of the cell. Thus, the aspect of the specimen in figures 12-14 corresponds to the dorsal view (nucleus in the right side of the cell). This specimen was later successfully transferred to a glass slide and observed under a microscope with D.I.C. The specimen appeared in the same view, also with the nucleus in the right side of the cell, but the TF was now displaced from the groove and a higher proportion of the TF was seen moving freely (Fig. 15).

D.I.C photomicrographs of a second specimen with the nucleus in the left side of the cell were taken (Figs 16-21). Figures 16-17 show a similar focus (both right antapical and the left lateral antapical extension in focus), with the TF located along the groove. The TF did not arise from the rear focus of the cell. Figure 18 shows, in a different focal plane, the left antapical and the right lateral antapical extensions, with the TF visible in the right side of the cell along the groove. The end of the TF was located in the central part of the cell (see also fig. 21). We were unable to focus on the area of the TF origin. The flagellum did not arise from the back of the cell (Figs 16-17). This position, with the nucleus in the left side of the cell, is the ventral view. After these observations the specimen was shaken until the TF was partially separated from the cingulum. The TF turned around the left side of the cingulum (Figs 19-20) (rear of the cell, as in Fig. 16). At a different focal plane most of the TF was visible (Fig. 21). The aspect of this specimen, with the nucleus in the left side, corresponds to the ventral view (Figs 16-21).

A third specimen with the nucleus in the right side was also observed with D.I.C. optics (Figs 22, 24) and inverted microscopy (Fig. 23). A part of a flagellum that could correspond to the longitudinal flagellum was observed between the two antapical extensions (Fig. 22). The TF ran along the cingulum in a frontal focus (Fig. 24). This position, with the nucleus in the right side, corresponds to the dorsal view.



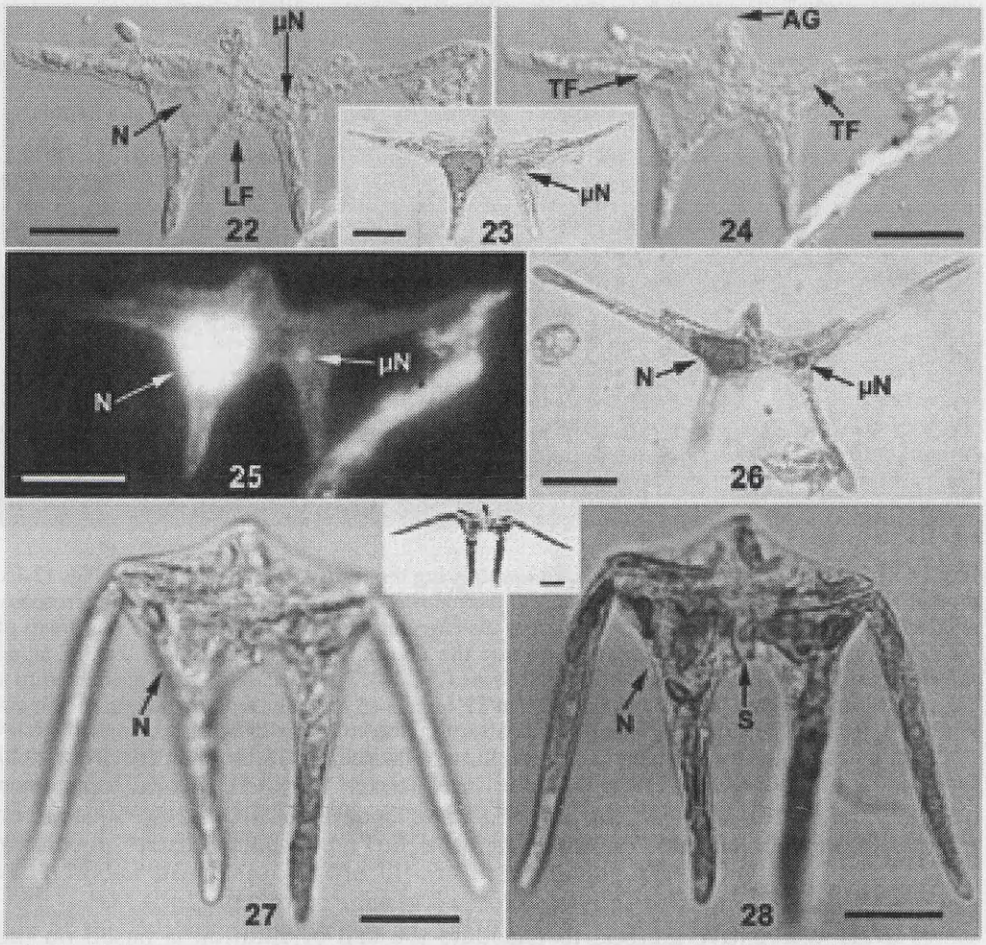
Figs 12-21. Photomicrographs of *Brachidinium* showing the transverse flagellum (TF). Figs 12-15. Dorsal view of a specimen under inverted microscopy (Figs 12-14), and direct microscopy (Fig. 15). See the end of the TF displaced from the cingulum and free moving in the rear focus of the cell (Fig. 12). See the cingulum groove where the TF ran (Fig. 13). Please note that TF along the cingulum does not arise from the frontal focus (Fig. 14). The specimens was transferred to a glass slide and observed with D.I.C. optic when TF appeared partially separated from the cingulum (Fig. 15). Figs 16-21. D.I.C. photomicrographs of the ventral view of other specimen. Figs 16-17 the TF ran all along the cingulum in the rear focus of the cell. Fig. 18. the end of the TF was observed in the central part of the cingulum in the frontal focus of the cell. Figs 19-21. The specimen was shaken until the TF was partially displaced from the cingulum in the rear focus (Figs 19-20) and the frontal focus (Fig. 21). AG= Apical groove; N= dinokaryon nucleus; TF = transversal flagellum. Scale bars 20 μm.

An alternative method to elucidate the cell orientation is based on the location of the sulcus (ventral side). The sulcus was not visible in the Lugol-fixed specimens, but was visible in the live specimen observed with a direct microscope. The nucleus of this specimen was located in the right side of the cell (Figs 27-28). Figure 27 focusses on only one of the four extensions, corresponding to the front of the specimen. Figure 28, showing three extensions in focus (closer to the glass slide), corresponds to the rear of the cell, with the sulcus being visible. Figures 27-28, with the nucleus in the right side of the cell, correspond to the dorsal view.

In these four specimens, based on the transverse flagellum or the sulcus, the ventral view corresponds to the nucleus being on the left side of the cell (Figs 29-30). The occurrence of a sulcus (Fig. 28) provides evidence of the existence of the longitudinal flagellum in the genus *Brachidinium* (partially observed in Fig. 22). This orientation is contrary to Fensome *et al.* (1993, p. 3, 56). Taylor (1980, p. 67) reported an illustration of *Brachidinium* with a weakly defined sulcus in the left side of the cell (Fig. 9). From our observations, however, the sulcus is centrally located in *Brachidinium* (Fig. 28).

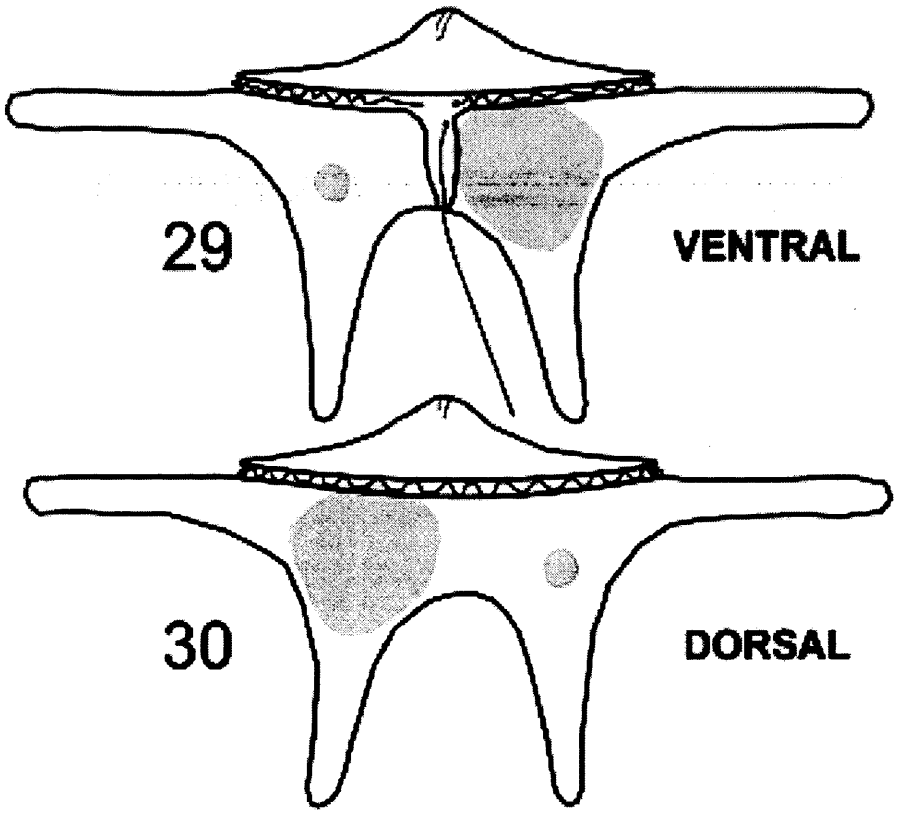
Binucleate specimens

The nucleus of *Brachidinium* was relatively large, ovoid, and occupied a significant proportion of the body cell. It was clearly visible in Lugol-fixed speci-



Figs 22-28. Figs 22-25. Dorsal view of a specimen. Figs 22, 24. D.I.C. photomicrographs. Fig. 22. See a part of a flagellum, possibly the longitudinal flagellum. Fig. 23. Inverted microscopy photomicrograph of the specimen. The arrow indicates the micronucleus (μN) or secondary nucleus. Fig. 24. Frontal focus showing the TF along the cingulum. Fig 25. Epifluorescence photomicrograph of the same specimen stained with DAPI and illuminated with U.V. light. The arrow indicates the secondary nucleus. Fig. 26. Inverted microscopy photomicrograph of other specimen in dorsal view. The arrow shows the secondary nucleus. Figs. 27-28. Photomicrographs of the dorsal view of a specimen observed live. Fig. 27. Frontal focus. Fig. 28. Rear focus. See the sulcus. An inset between the figures 27-28 shows a low magnification photomicrograph taken prior to the movement of the lateral extensions of the specimen; AG = Apical groove; N = dinokaryon nucleus; μN = secondary nucleus; TF = transversal flagellum; LF = longitudinal flagellum; S = sulcus. Scale bars 20 μm.

mens and appears darker than the rest of the cell surface (e.g., Figs 14, 23, 26), whereas it was less visible in the cell observed live (Figs 27-28). The dinokaryon nucleus was confirmed by DAPI-staining (Fig. 25). In addition, several of the Lugol-fixed specimens showed a secondary small nucleus in side of the cell opposite the dinokaryon nucleus, with both nuclei staining the same dark brown colour (Fig. 26). In a DAPI-stained specimen (Figs 22-24), the micronucleus fluoresced



Figs 29-30. Line drawings of the ventral (Fig. 29) and dorsal (Fig. 30) views in *Brachidinium*.

when excited with U.V. light and the dinokaryon nucleus appeared brighter than the micronucleus (Fig. 25). Sournia (1972) did not find chloroplasts in *B. brevipes*. Sournia (1972) and Léger (1972) reported one circular 'plast' in the opposite side of the nucleus in their line drawings (Fig. 8 and Léger (1972, p. 29)). This could be interpreted as the first evidence of the occurrence of a secondary nucleus in *Brachidinium*.

The occurrence of binucleate dinoflagellates is very rare. The freshwater dinoflagellate *Kryptoperidinium foliaceum* (Stein) Lindemann presented mononucleate and binucleate strains. *Kryptoperidinium foliaceum* contained a fucoxanthin-containing diatom as a cytoplasmic endo-symbiont (Kempton *et al.*, 2002). The origin of the secondary nucleus in *Brachidinium* was not clarified in the present study.

Live cell and moveable extensions

The extensions in *Brachidinium* are moveable, as reported by Léger (1971), based on observations by Cachon on a live specimen collected from Villefranche-sur-Mer (Ligurian Sea). We include, for the first time, photomicrographs of a live specimen of *Brachidinium*. During our microscopical observations,

the specimen moved the lateral antapical extensions from the initial position parallel to the cingulum (see inset between the figure 27 and 28), to a final position with the two lateral extensions aligned with the two central antapical extensions (Figs 27-28). This last appearance was not found in our observation of the Lugol-fixed specimens. Sournia (1972) has reported different angles of the lateral extensions from fixed specimens (Figs 5-6). The movement occurred when the specimen was observed at a high magnification with high light intensity, and took about 10 seconds.

The changes in the shape of this live specimen of *Brachidinium*, and the common changes of morphology during the life cycle of unarmoured dinoflagellates with elongate extensions (e.g., Konovalova, 2003) cast some doubts on the validity of all species of *Brachidinium* other than the type. The type species of the closely related genus *Asterodinium* is also supposed to show a high morphological variability (Gómez, 2003a). Most records of *Brachidinium* are from the 1970s, and species such as *B. catenatum* (Fig. 4) and *B. brevipes* (Fig. 8) have not been reported after the initial descriptions. The description of *Brachidinium brevipes*, with a rough surface, is based on morphological features that can be considered as intraspecific variables in other dinoflagellates. The morphology of *Brachidinium taylorii* (Fig. 7) is the same as some forms of *B. capitatum*. *Brachidinium catenatum* (Fig. 4) is a doubtful taxon according to Taylor (1967). *Brachidinium capitatum* requires further studies on the morphological variability as well as for unique characteristics such as secondary nuclei and moveable extensions.

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Is *Karenia* a synonym of *Asterodinium-Brachidinium* (Gymnodiniales, Dinophyceae)?

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From material collected in open waters of the NW and Equatorial Pacific Ocean the detailed morphology of brachidiniaceans based on two specimens of *Asterodinium gracile* is reported for the first time. SEM observations showed that the straight apical groove, the morphological characters and orientation of the cell body were similar to those described for species of *Karenia*. *Brachidinium* and *Asterodinium* showed high morphological variability in the length of the extensions and intermediate specimens with *Karenia*. *Karenia*-like cells that strongly resemble *Brachidinium* and *Asterodinium* but lacking the extensions co-occurred with the typical specimens. The life cycle and morphology of *Karenia papilionacea* should be investigated under natural conditions because of the strong similarity with the brachidiniaceans.

Key words: Phytoplankton, *Asterodinium*, *Brachidinium*, Brachydinium, *Gymnodinium*, *Karenia*, Dinophyta, apical groove, SEM, Pacific Ocean.

Introduction

Fixatives, such as formaline or Lugol, do not sufficiently preserve unarmoured dinoflagellates to allow species identification. Body shape and morphology often change during the process of fixation so that even differentiating between the genera *Gymnodinium* Stein and *Gyrodinium* Kofoid *et* Swezy is difficult (ELBRÄCHTER 1979). Most of the original descriptions, often based on fixed specimens, were insufficiently detailed and the morphological characters for the differentiation of the species were sparse. TAKAYAMA (1985) developed a scanning electron microscopy (SEM) technique that allowed the observation of the apical grooves (acrobase) in some gymnodinioid cells. A revision by DAUGBJERG et al. (2000) combined large subunit (LSU) rDNA sequences, ultrastructure and chloroplast

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pigment composition, which allowed for the division of the large heterogeneous genus *Gymnodinium* into four genera: *Gymnodinium* sensu stricto, with a horseshoe-shaped apical groove and peridinin as the main carotenoid; *Akashiwo* G. Hansen *et* Moestrup, with a clockwise spiral apical groove and peridinin; *Karenia* G. Hansen *et* Moestrup, with a straight apical groove and fucoxanthin; and *Karlodinium* J. Larsen, with a short straight apical groove, a ventral pore, and fucoxanthin. Later the genus *Takayama* de Salas, Bolch, Botes *et* Hallegraeff, with sigmoid apical grooves, was also erected (DE SALAS et al. 2003). Since then, the description of new species of the genus *Karenia* has proliferated (e.g., BOTES et al. 2003; HAYWOOD et al. 2004). Unialgal cultures have been established by isolation of vegetative cells from coastal waters and maintained under laboratory conditions. The abundant material available allows detailed studies on the ultrastructure, pigment and toxin composition and molecular phylogeny. Little is known on the morphology and the life cycle of these species under natural conditions.

There are few records of gymnodinioid cells identified at the species level in open waters. Morphological characters such as the occurrence of body extensions facilitate identification under routine analysis in taxa such as *Gyrodinium falcatum* Kofoid *et* Swezy (=*Gymnodinium fusus* Schütt pro parte). Observations of live specimens of *G. falcatum* from natural samples (ELBRÄCHTER 1979; YOSHIMATSU 1990) or temporal cultures (KONOVALOVA 2003) showed high morphological variability and fast changes of cell shape and length of extensions. Stages of the life cycle of *G. falcatum* were described as separate species, such as *Pseliodinium vaubanii* Sournia (KONOVALOVA 2003).

The occurrence of extensions is the main character of the unarmoured genera *Brachidinium* F.J.R Taylor and *Asterodinium* Sournia, which species were described from single or a few preserved specimens. The only known morphological characters of the brachidiniaceans were the pronounced compressed cell body, yellow-green chloroplasts and the prominent nucleus. Despite the lack of morphological data, the order Brachidiniales A.R. Loeblich III *ex* Sournia was established exclusively for these genera. No photomicrographs of *Asterodinium* were available in the literature. From Mediterranean, Atlantic and Pacific waters, GÓMEZ (2003) reported a high variability in the length of the extensions among the specimens of *Asterodinium*. Within this context, GÓMEZ (2003, p. 339) concluded: »Further research should address the *Asterodinium gracile* complex; does it constitute one species with high morphological variability, depending on environmental conditions, or are different species involved?«

Brachidinium is more commonly recorded than *Asterodinium* and one section plot of its distribution is even available (MARGALEF 1975). *Brachidinium* also showed a high variability in the length and relative position of the extensions, being often reported as *Brachidinium* sp. because the specimens cannot be ascribed to any known species. No detailed study on the morphological characters of *Brachidinium* was available. From Lugol-fixed specimens and one live specimen, GÓMEZ et al. (2005) reported details of the morphology of *Brachidinium*. SOURNIA described 4 of the 5 species of brachidiniaceans. From the same samples of his records, SOURNIA illustrated gymnodinioid cells that he considered close to *Brachidinium* (SOURNIA 1972, p. 157). Later SOURNIA (1986) hypothesized that the Brachidiniales constitute a part of the life cycle of more common dinoflagellates.

Despite the scarcity of specimens of brachidiniaceans available and the delicacy of them, by using the TAKAYAMA'S method, we have successfully obtained the first SEM pic-

tures of a member of the order Brachidiniales based on two specimens of *Asterodinium gracile* Sournia. The morphological characters of *Asterodinium* were similar to those of some species of the genus *Karenia*. Gymnodinioid cells which appearance strongly resembled specimens of *Brachidinium* and *Asterodinium* but lacking the extensions co-occurred with the typical *Brachidinium* and *Asterodinium*. The life cycle and the morphology of some species of *Karenia* should be investigated under natural conditions because they may correspond to forms of *Brachidinium-Asterodinium*.

Material and methods

Sample collection and light microscopical observations were as in GÓMEZ et al. (2004, 2005). For SEM, specimens were isolated with a capillary from sedimentation chambers and adhered to poly-L-lysine-coated cover-slip. Fixed cells attached to the cover-slip were rinsed twice in distilled water for 5 min each. Cells were then dehydrated through an ethanol series, transferred into isoamyl acetate (TAKAYAMA 1998), dried in a critical point drier (HCP-2, Hitachi, Japan), and coated with Au-Pd. Observations were made using SEM (S-430 and S-800, Hitachi, Japan).

Results and discussion

Asterodinium

The new records of *Asterodinium* from the western Pacific Ocean (Tab. 1) showed a high variability in the length of the extensions as previously reported by GÓMEZ (2003). Observations with Nomarski differential interference contrast (DIC) optics showed the transverse flagellum; however the insertion point was not clearly revealed (Figs. 1, 2). With SEM, the insertion point was observed in two specimens of *Asterodinium gracile* (Figs. 8–15). The ventral view corresponded to the nucleus in the left hyposome. The me-

Tab. 1. Records of *Asterodinium* from the Pacific Ocean. Date, depth (m), geographic coordinates (latitude, longitude), and dimensions: width at the level of the cingulum (μm); total length (μm) of each record. Records from the vicinity of the Kuroshio Current can be found in GÓMEZ (2003). *Karenia*-like cells are omitted.

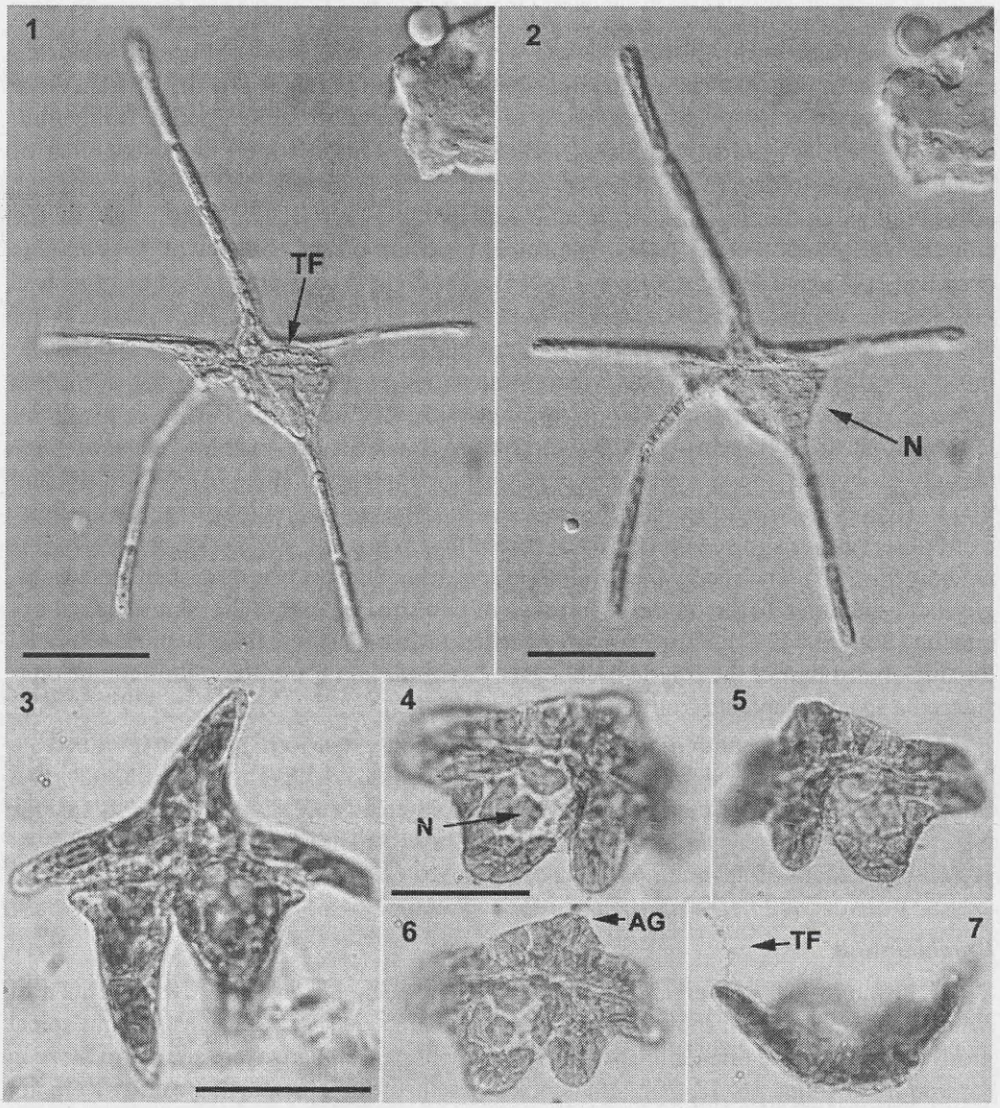
Taxon	Date	Depth	Latitude	Longitude	Wide	Length
Asterodinium gracile	16 Nov 2002	50	5°11'N	124°05'E	25	65
Asterodinium gracile (Figs 8–15)	16 Nov 2002	50	5°11'N	124°05'E	23	55
Asterodinium gracile (Fig. 3)	17 Nov 2002	30	5°N	121°E	28	55
Asterodinium gracile	17 Nov 2002	75	5°N	121°E	23	60
Asterodinium gracile	19 Nov 2002	75	7°25'N	121°12'E	20	100
Asterodinium gracile	19 Nov 2002	50	7°25'N	121°12'E	24	105
Asterodinium gracile	03 Dec 2002	30	8°50'N	121°48'E	20	–
Asterodinium gracile	18 Jan 2003	120	0°	170°E	21	110
Asterodinium gracile	17 Jan 2003	100	0°	165°E	22	60
Asterodinium sp. (Figs 4–7)	23 Jan 2003	120	0°	170°W	32	–

dian cingulum was descending and displaced by the cingulum width (Figs. 10, 14). The longitudinal flagellum was not observed with SEM, having probably been lost during sample preparation. The cavity that appeared below the terminal part of the transverse flagellum might correspond to the place of the insertion of the longitudinal flagellum (Figs. 11, 15). A vertically oriented cingular ridge runs between the two points of flagellar insertion (Fig. 15). The ventral ridges are present in species of *Karenia* and have an intercingular tubular structure that traverses the proximal and distal ends of the cingulum (HAYWOOD et al. 2004). The sulcal intrusion on the epitheca of *A. gracile* is open and extends to left of the apex (Fig. 14). A straight groove with rolled margins was visible in the central apical extension of both specimens (Figs. 9, 13). The sulcus was not well defined under SEM (Figs. 11, 15). These morphological characters were similar to those described for *Karenia papilionacea* Haywood *et* Steidinger or *K. bicuneiformis* Botes, Sym *et* Pitcher (=*K. bidigitata* Haywood *et* Steidinger) (BOTES et al. 2003; HAYWOOD et al. 2004). In *Asterodinium gracile* the carina or apical protrusion is extremely elongated and is named the central apical extension (Fig. 23). With DIC and SEM, trichocysts were observed in *Asterodinium gracile*, sometimes forming clusters. SEM observations showed that the basal part of the trichocysts was thicker that the terminal hair (Fig. 13). The species *Asterodinium spinosum* Sournia was described from a single fixed specimen based on the occurrence of two small spines in the central apical extension (SOURNIA 1972). However, the present study reveals that these »spines« may be the thick basal part of the fragile trichocysts. *Asterodinium spinosum* should not be considered a species separate from the type species.

One of the specimens of *Asterodinium* showed short extensions, being an intermediate between the typical *Asterodinium* and the *Asterodinium* that lacks any extensions (Fig. 3). Strongly dorso-ventrally compressed gymnodinioid cells with short lobulate extensions were observed showing the distinctive chloroplasts, the straight apical groove and the prominent nucleus of *Asterodinium* (Figs. 4–7).

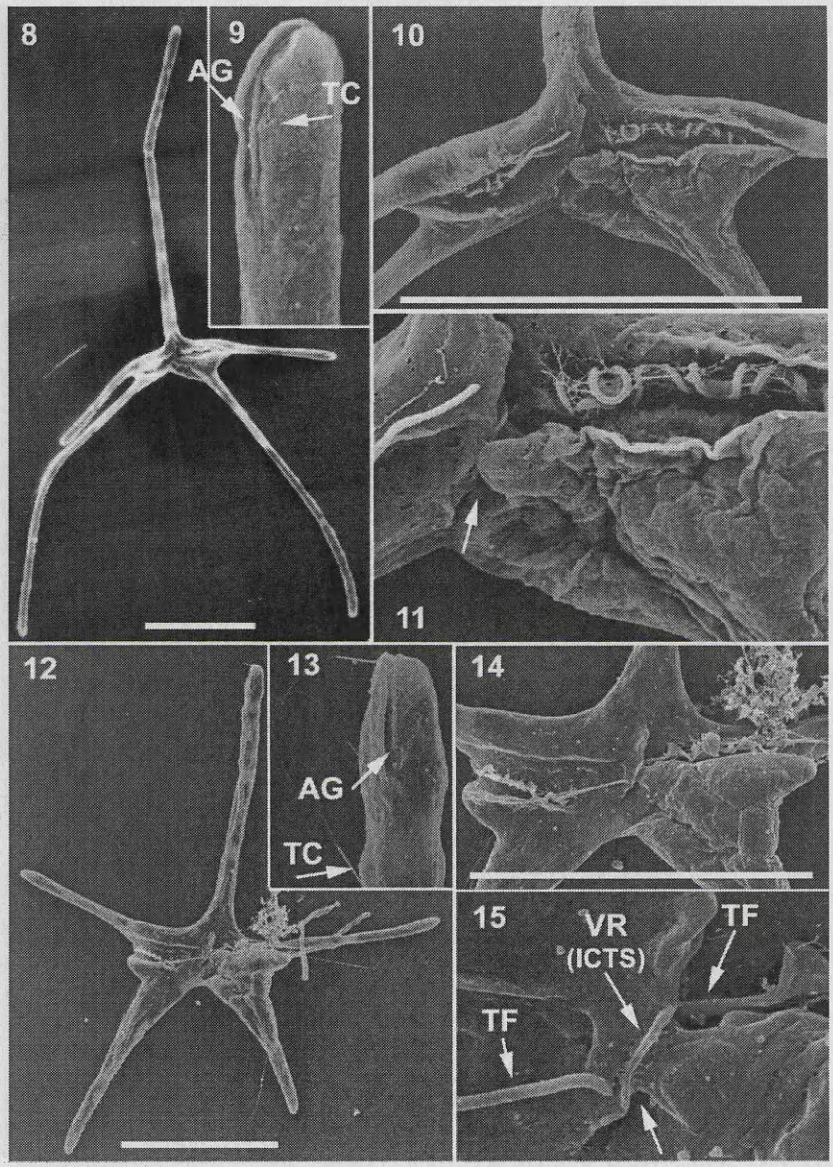
Brachidinium

Light microscopy observations of Lugol-fixed specimens and one live specimen of *Brachidinium capitatum* showed morphological characters such as a short straight apical groove (Fig. 20). The orientation and morphology of the cell body were similar to those in *Asterodinium* (Figs. 16, 18, 20), although the details of the intercingular region were not clearly visible. Several of the specimens of *B. capitatum* showed a darker area in the right hyposome (Figs. 16, 18, 26). This region appeared with a variable size and colour, often similar to the brown colour of the nucleus of the Lugol-fixed specimens. After DAPI-staining this region fluoresced when excited with UV light but less bright than the dinokaryon. GÓMEZ et al. (2005) interpreted this darker area as a secondary nucleus in *B. capitatum* as occurred in some freshwater dinoflagellates. However this region varied in size, shape and colour among the Lugol-fixed specimens (Figs. 16, 18) more than would be expected for a secondary nucleus. The occurrence of an accumulation body in the right hyposome of *B. capitatum* appeared a more probable explanation. The role of the accumulation bodies in dinoflagellates is poorly understood. It is believed to be in an endocytic pathway functioning as a lysosome (ZHOU and FRITZ 1994). Among the species of *Karenia*, *K. papilionacea* was also characterised by an accumulation body that was visible in the right hyposome in 10% of cells under culture (HAYWOOD et al. 2004).



Figs. 1–7. DIC photomicrographs of the ventral view of *Asterodinium gracile* in different focuses (30°N; 138°E, 80 m depth). See the nucleus in the left hyposome and the transverse flagellum. Figs. 3–7. LM micrographs of *Asterodinium*. Fig. 3. Specimen of *Asterodinium* in ventral view with short extensions from the Celebes Sea. Figs. 4–7. Specimen of *Asterodinium* with lobulate extensions from the Central Equatorial Pacific. Figs. 4, 6. Dorsal views. Figs. 5, 7. Ventral and lateral views respectively. The arrows point to the nucleus, transverse flagellum and the apical groove (acrobase). AG=apical groove; TF= transverse flagellum; N=nucleus. Scale bars = 20 μm.

Large extensions are one of the main characteristics of the Brachidiniales. Specimens lacking the extensions are hard to assign to *Brachidinium* or *Asterodinium* and are consequently pooled as unidentified gymnodinioid cells under routine microscopical analysis of fixed phytoplankton. In the present study gymnodinioid cells that strongly resembled



Figs. 8–15. SEM pictures of two specimens of *Asterodinium gracile* in the ventral view. Figs 8–11. Specimen with long extensions collected from the Kuroshio Current region (33° 30'N; 138°E, 100 m depth). Fig. 9. Detail of the central apical extension. See the straight apical groove or acrobase and the trichocyst pores. Figs. 10–11. Detail of the central body and the location of the insertion of the transverse flagellum. Fig. 11. The arrow points to a cavity where the longitudinal flagellum might arise. Figs. 12–15. Specimen with shorter extensions collected from the Celebes Sea (5°11'N; 124°05'E, 50 m depth). Fig. 13. Detail of the central apical extension. See the apical groove and trichocysts. Figs. 14–15. Detail of the central body. Fig. 15. A ventral ridge runs between the two points of flagellar insertion. The arrow below the ventral ridge points to a cavity where the longitudinal flagellum might arise. AG=Apical groove; TF=transverse flagellum; TC=trichocyst; VR=ventral ridge; ICTS= Intercingular tubular structure. Scale bars = 20 μm.

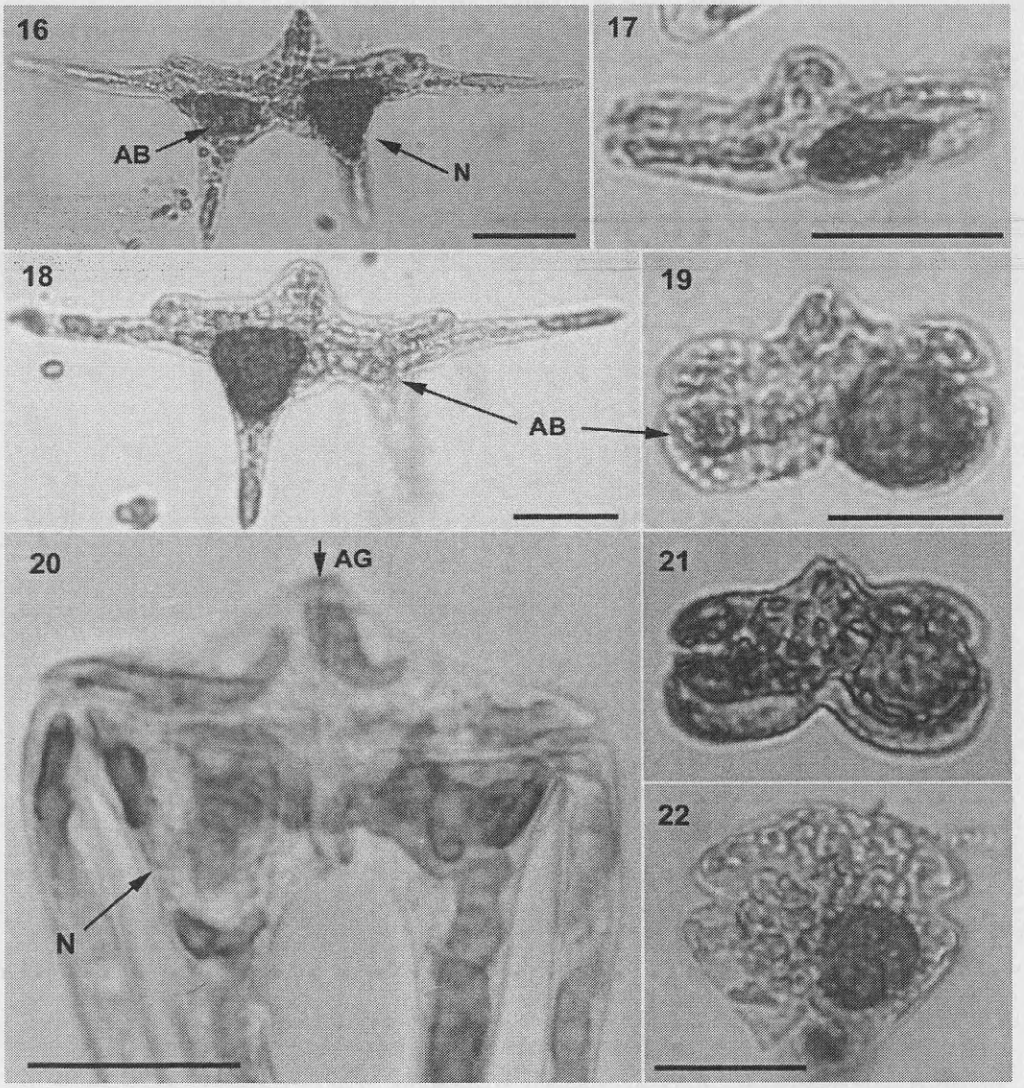
B. capitatum cells lacking the extensions co-occurred with the typical *B. capitatum* (Figs. 17, 19, 26). Several of the typical *B. capitatum* showed accumulation body of variable size and colour in the right hyposome (Figs. 16, 18), which was also visible in the specimens lacking the extensions (Fig. 19). These gymnodinioid cells were also reported in previous studies including records of *B. capitatum*. In the SW Indian Ocean, SOURNIA (1972) described two new species of *Brachidinium* and also found the type species with variable morphology. From the same samples, SOURNIA illustrated gymnodinioid cells that he considered close to *Brachidinium* (Fig. 25). Observations of live specimens of *Brachidinium* (LÉGER 1971; GÓMEZ et al. 2005) have even showed the extensions to be moveable. In cultures, the carina of *Karenia papilionacea* contracts forward when the cells are stressed (HAYWOOD et al. 2004, p. 170). SOURNIA (1972, p. 157) also illustrated the gymnodinioid cell folded with the carina contracted forward (Fig. 25). *Brachidinium capitatum* (Fig. 26) and *K. papilionacea* co-occur in the coastal waters of the south of Japan (misidentified as *Karenia brevis* (Davis) G. Hansen *et* Moestrup) and in other warm to temperate waters (IIZUKA 1976; HAYWOOD et al. 2004). From the eastern Mediterranean Sea, ABBOUD-ABI SAAB (1989) found *B. capitatum* and also illustrated several unidentified gymnodinioid cells with similar morphology to the *Karenia*-like cells reported in SOURNIA (1972) and in the present study (Figs 17, 19). *Karenia papilionacea* and *B. capitatum* are both cosmopolitan taxa that appear in surface waters in low abundance (MARGALEF 1975; HAYWOOD et al. 2004).

In the table 2 the morphological and ecological characters of *B. capitatum* and *K. papilionacea* have been compared. The distinctive morphological characters of *K. papilionacea* coincided with *B. capitatum* (Tab. 2, Figs 16–20). The *Karenia*-like cells that co-occurred with *B. capitatum* showed morphology similar to that of the Lugol-fixed cells of the culture of *K. papilionacea* at the Cawthron Institute, New Zealand (Fig. 21).

According to HAYWOOD et al. (2004), *Karenia bicuneiformis* (=*K. bidigitata*) often co-occurs with *K. papilionacea*. In the present study several specimens were tentatively identified as *K. bicuneiformis*, also co-occurring with *B. capitatum* and the *Karenia*-like cells (Fig. 22). *Karenia papilionacea* and *K. bicuneiformis* are very close from morphological and phylogenical points of view (HAYWOOD et al. 2004).

No studies are available on the projection of the cell body extensions in unarmoured dinoflagellates. ZIRBEL et al. (2000) reported that the length of the extensions of the armoured dinoflagellate *Ceratocorys horrida* Stein varied as an adaptive strategy according to water motion. Specimens lacking the extensions appeared as early as 1 h after an increase in turbulence. Cells with long extensions were transforming into cells with short or no extensions. This phenomenon was reversible and the extensions reappeared after a reduction in turbulence (ZIRBEL et al. 2000).

The expansion of the cell body with the projection of extensions is expected to be easier for unarmoured dinoflagellates. Beyond the high shape plasticity with fast contractions of the carina of *K. papilionacea*, a high variability in cell size in cultures is also observable. HAYWOOD et al. (2004, p. 175) reported, »Cellular size measurements are given as ranges, reflecting small to large cells present in cultures that were not separated into size classes because of the intergradations between sizes and because the significance of the size classes cannot be addressed until the life cycle of these species is known«.

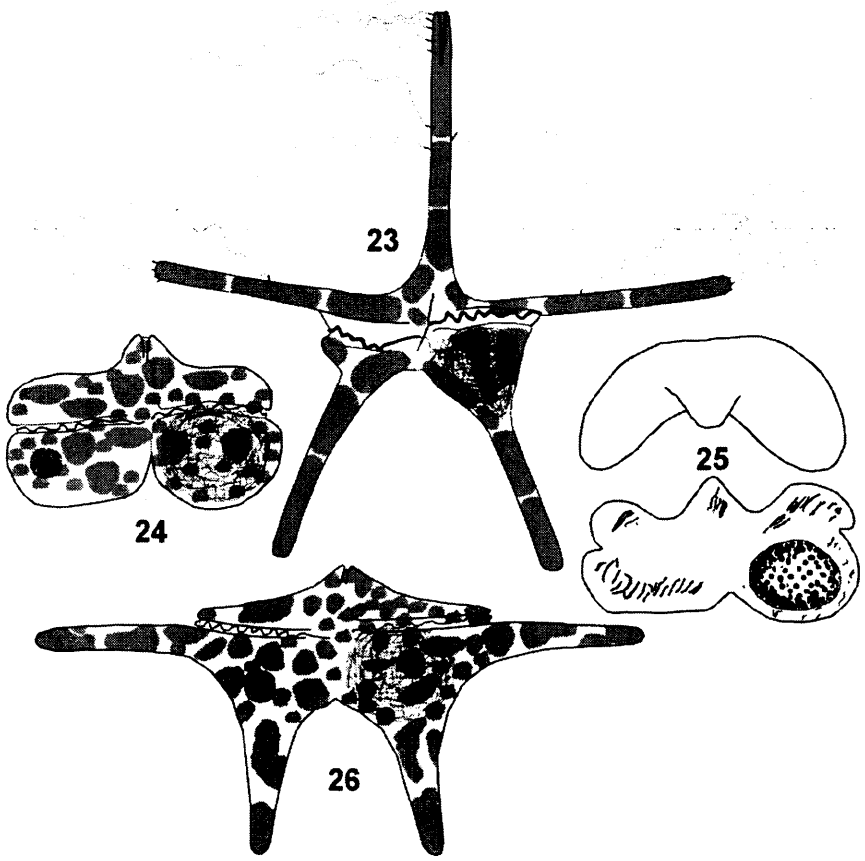


Figs. 16–22. LM micrographs of *Brachidinium capitatum* with and lacking the extensions, *Karenia papilionacea* and *K.* cf. *bicuneiformis* (=*K. bidigitata*). All Lugol-fixed specimens except Fig. 20. Fig. 16. Ventral view of a specimen of *Brachidinium* with a prominent accumulation body from the Philippine Sea (32°N; 138°E, 30 m depth). Fig. 17. *Karenia*-like cell that strongly resembles *Brachidinium* but lacking the extensions (32°N; 138°E, 80 m depth). Fig. 18. Dorsal view of a specimen of *Brachidinium* with a less marked accumulation body (0°; 160°E, 0 m depth). Fig. 19. *Karenia*-like cell from the same sample as figure 16 with an accumulation body (32°N; 138°E, 30 m depth). Fig. 20. Back focus of the cell body of a live specimen of *B. capitatum* in the dorsal view (see GÓMEZ et al. 2005). Fig. 21. Lugol-fixed specimen of *K. papilionacea* from the culture of the Cawthron Institute, New Zealand. Fig. 22. Tentatively *Karenia bicuneiformis* (=*K. bidigitata*) (0°; 175°E, 15 m depth). AB=accumulation body; AG=Apical groove; N=nucleus. Scale bars = 20 μm.

Tab. 2. Comparative morphological and ecological characteristics of *Brachidinium capitatum* (Lugol-fixed specimens from open waters and one live specimen from the coastal waters of Japan). Data from *Karenia papilionacea* (from cultures) based on HAYWOOD et al. (2004).

Character	*Brachidinium capitatum*	*Karenia papilionacea*
Apical groove	Straight, very short and bisects the carina	Straight, very short and bisects the carina
Carina (apical protrusion)	Pointed	Pointed
Dorsoventral compression	Moderate	Moderate
Nucleus shape	Spherical to slightly oval	Spherical to slightly oval
Nucleus location	Left hyposome	Left hyposome
Hyposome shape	Bilobed, centrally excavated	Bilobed, centrally excavated
Hyposome excavation	Pronounced	Pronounced
Cell width at the cingulum level	25–55 μm	18–48 μm
Cingulum	Median, descending and displaced by the cingulum width	Median, descending and displaced by the cingulum width
Sulcal intrusion on the epitheca	No visible from Lugol-fixed specimens	Open sulcus extends to left of apex
Chloroplast number	Many	Typically 2–20 chloroplasts per cell
Chloroplast shape	Round to reniform in cell body, elongate plastids in the extensions	Round to reniform
Chloroplast colour	Yellow-green	Yellow-green
Fucoxanthin	No tested	yes
Accumulation body occurrence	~25% of the specimens in nature	10% of the specimens in culture
Accumulation body number	1	1
Accumulation body location	Right hyposome	Right hyposome
Accumulation body shape	Spherical to oval	Spherical to oval
Accumulation body size	Variable	Variable
Cell movements	Carina and extensions change of shape and length	Carina contracts forward to overlap the epitheca
Geographical distribution	Cosmopolitan (temperate to warm)	Cosmopolitan (temperate to warm)
Ecological distribution	Surface, coastal to open waters (MARGALEF 1975)	Surface, coastal to open waters
Abundance in natural waters	Low (MARGALEF 1975)	Low (<1000 cells L^{-1})
Period of max. abundance	Summer	Summer
Life cycle	Unknown	Unknown

The life cycle and morphology of species such as *K. papilionacea* should be investigated under natural conditions because they may correspond to a life stage of brachidiniaceans. There are no reasons to retain the order Brachidiniales because the morphological characters of *Brachidinium-Asterodinium* do not differ from those in *Karenia*.



Figs. 23–26. Line drawings of *Asterodinium*, *Brachidinium* and the related *Karenia* cell. Fig. 23. Typical *Asterodinium gracile*. Fig. 24. *Karenia*-like cell related to the brachidiniaceans. Fig. 25. Two views of the *Karenia*-like cell related to *Brachidinium* according to SOURNIA (1972, p. 157). Fig. 26. Typical *Brachidinium capitatum*.

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The Dinoflagellate Genera *Brachidinium, Asterodinium, Microceratium* and *Karenia* in the Open SE Pacific Ocean

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The morphometry and distribution of the unarmoured dinoflagellates *Brachidinium capitatum* F.J.R. Taylor, *Asterodinium gracile* Sournia, *Microceratium orstomii* Sournia and the toxic species *Karenia papilionacea* Haywood *et* Steidinger have been investigated in open waters of the SE Pacific Ocean. The genus *Microceratium* Sournia is recorded for the first time since the initial description. These taxa showed a high morphological similarity and they may correspond to life stages of a highly versatile single species that is able to project body extensions. *Karenia papilionacea* showed the higher abundance in the surface waters of the more productive areas (the Marquesas Archipelago and the Perú-Chile Current). *Brachidinium capitatum* and *K. papilionacea* often co-occurred, predominating *B. capitatum* in offshore surface waters. *Asterodinium gracile* was recorded at the bottom of the euphotic zone (down to 210 m depth), with a shallower distribution in more productive areas. Intermediate specimens of *Asterodinium-Brachidinium-Karenia*, with variable disposition and size of the body extensions were illustrated.

Key Words: *Asterodinium, Brachidinium,* harmful algae bloom, *Karenia papilionacea, Microceratium,* phytoplankton, SE Pacific Ocean

INTRODUCTION

Most of the species of the genus *Gymnodinium* Stein were described during the late 1800's and early 1900's. Very little progress has been made since then and the taxonomic system has therefore remained almost unchanged since the 19th century. Biecheler (1934) using a silver-impregnation method observed for the first time the apical groove in *Gymnodinium*. Takayama (1985) based on scanning electron microscopy (SEM) showed several types of apical grooves in unarmoured dinoflagellates. Daugbjerg *et al.* (2000) based on light microscopy, SEM, pigment composition and LSU rDNA sequences split *Gymnodinium* into four genera: *Gymnodinium sensu stricto, Akashiwo* G. Hansen *et* Moestrup, *Karlodinium* J. Larsen and *Karenia* G. Hansen *et* Moestrup. Since then, the description of new species of *Karenia* characterized by a short straight apical groove, with fucoxanthin and lacking peridinin, has proliferated. In some cases, a single species has been described under different names such as *K. bicuneiformis* Botes, Sym et Pitcher and *K. bidigitata* Haywood *et* Steidinger and other taxa may be conspecific such as *K. longicanalis* Yang, Hodgkiss *et* G. Hansen and *K. umbella* de Salas, Bolch *et* Hallegraeff (Yang *et al.* 2001; Botes *et al.* 2003; de Salas *et al.* 2004; Haywood *et al.* 2004).

Among the recently described species, *Karenia papilionacea* Haywood *et* Steidinger showed several peculiar characteristics in cultures with an unusual plasticity and high size variability. In culture, *K. papilionacea* is also able to move forward the prominent apical process (Haywood *et al.* 2004, p. 170). Other close species, *K. bicuneiformis*, showed pointed or bulbaceous antapical tips in natural waters that were rounded when the species is cultured (Haywood *et al.* 2004, p. 173). The species of *Karenia* were described based on abundant materials cultured under optimal conditions for growth that does not reproduce the low turbulence and oligotrophic conditions of the open ocean. Consequently little is known on the morphology and the life cycle of species such as *K. papilionacea* under natural conditions.

The dinoflagellate *Brachidinium capitatum* F.J.R. Taylor is a flattened unarmoured taxon easily identifiable by the four radiating elongate antapical extensions, apical process, numerous yellow-green chloroplasts and promi-

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nent nucleus. However, the partially erroneous description by Taylor (1963) based on formalin-preserved specimens induced a mysterious character to *Brachidinium* F.J.R. Taylor. Taylor described *Brachidinium* as a laterally compressed, with no cingulum or sulcus, non-motile dinoflagellate placed in the order Dinococcales Pascher (coccoid or parasitic dinoflagellates). Sournia (1972b) found more specimens of *B. capitatum* with variable morphology and based on single or a few fixed specimens described two new species: *B. taylorii* Sournia and *B. brevipes* Sournia. From the same location, Sournia (1972a, b) described two closely related genera: *Asterodinium* Sournia with the species *A. gracile* Sournia and *A. spinosum* Sournia and *Microceratium* Sournia with the species *M. orstomii* Sournia. *Asterodinium* differs from *Brachidinium* on having two elongate extensions radiating from the hyposome and three extensions from the episome. In comparison with *Asterodinium, Microceratium* Sournia has only one extension in the episome and two extensions in the hyposome. Co-occurring with these records, Sournia found gymnodinioid cells that he considered close to *Brachidinium*, illustrating the species recently described as *Karenia papilionacea* (Sournia 1972b, p. 157; Haywood *et al.* 2004, p. 171). Later Sournia (1986, p. 49) with the sentence "il pourrait s'agir ici de stades de développement d'autres dinoflagellés plus notoires" was hypothesizing that the brachidiniaceans, members of the genera *Brachidinium, Asterodinium* and *Microceratium*, constitute life stages of more common dinoflagellates.

The brachidiniaceans have remained under-investigated during decades. Gómez *et al.* (2005a, b) based on light and scanning electron microscopy revealed the morphological similarities among *Brachidinium capitatum, Asterodinium gracile* and *Karenia papilionacea*. These three taxa coincided in distinctive morphological characters such as the straight apical groove, cingulum-sulcus juncture, prominent nucleus in the left hyposome, numerous yellow-green chloroplasts, among other characters (Gómez *et al.* 2005b). Consequently the Sournia's (1986) hypothesis reappeared and the brachidiniaceans may be life stages of common coastal species that are able to project body extensions. In coastal waters, brachidiniaceans with no extensions may be polled as unidentified gymnodinioid cells under routine microscopical analysis or refereed as *Karenia brevis*-like cells before the description of *K. papilionacea* (Iizuka 1975; Fraga and Sánchez 1985; Nézan 1998).

Within this context, a cruise along a transect of 7500 Km from the Marquesas Archipelago to the Chilean coasts through the severe oligotrophic waters of the South Pacific Gyre (Claustre and Maritorena 2003) provides the opportunity to investigate the distribution of the brachidinianceans and *K. papilionacea* under different trophic regimes. The present study also investigates the morphometry of *Brachidinium capitatum, Karenia papilionacea* and *Asterodinium gracile. Microceratium orstomii* has been recorded for the first time since the initial description. Intermediate specimens among these genera, with variable disposition and size of the body extensions are illustrated. The hypothesis of the conspecifity of these taxa is reported.

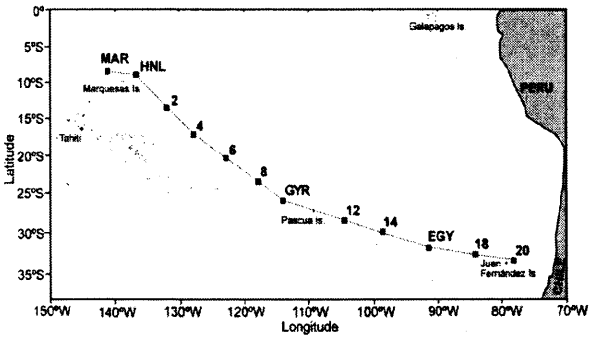

Fig. 1. Map of the sampling stations during the BIOSOPE cruise in the SE Pacific Ocean.

MATERIALS AND METHODS

Samples were collected at 12 stations from 5 to 270 m depth during the BIOSOPE (Biogeochemistry and Optics South Pacific Experiment) cruise on board *R/V L'Atalante* from 26 October to 12 December 2004 (Fig. 1). Eighty three samples collected by Niskin bottles were preserved with acidified Lugol's solution and stored at 5°C. Samples of 500 mL were concentrated via sedimentation in glass cylinders. Along 6 days, the top 450 mL of sample was progressively slowly siphoned off with small-bore tubing. Fifty mL of concentrate representing 500 mL whole water was settled in composite settling chambers. The entire chamber was scanned at 200× with an IX71 inverted Olympus microscope equipped with a DP70 Olympus digital camera and each specimen was photographed and measured at 400× with the DP70-BSW software (Olympus, Tokyo, Japan).

The percentage of surface irradiance at each depth was calculated from underwater PAR (Photosynthetic Active Radiation, 400-700 nm) profile performed by a PNF-300 Profiling Natural Fluorometer sensor (Biospherical Instruments, San Diego, U.S.A.). The limit of the euphot-

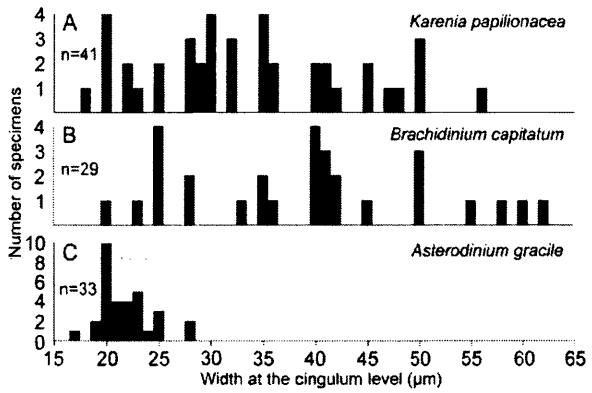

Fig. 2. Histograms of the width at the cingulum level of the records of A. *Karenia papilionacea*, B. *Brachidinium capitatum* and C. *Asterodinium gracile*.

ic zone corresponds to the depth where PAR is reduced to 1% of its surface value. The variables represented in the section plots were produced by interpolation between casts using the kriging as the gridding method in the Surfer software (Golden Software, Golden, U.S.A.).

RESULTS

Karenia papilionacea

A total of 41 specimens have been ascribed to the "standard" *K. papilionacea*. The width at the cingulum level ranged from 18 to 56 µm with an average width of 33.7 ± 10 µm (Fig. 2A). *Karenia papilionacea* and *B. capitatum* often co-occurred and the former predominated in the surface waters of productive regions (MAR and St. 20) whereas *B. capitatum* prevailed in oligotrophic offshore stations (Figs 3A, B). The highest abundance of *K. papilionacea*, 12 cells L^{-1}, was recorded at 15 m depth in open waters of the Perú-Chile Current near the Juan Fernández Archipelago and 8 cells L^{-1} near the Marquesas Archipelago (Fig. 3A). However, in these regions the abundance was higher if the specimens that cannot be strictly ascribed to *K. papilionacea* are included (Figs 4I, J)

Brachidinium and *Asterodinium* are easily identifiable due to the distinctive body extensions. The cell body of *K. papilionacea* corresponded to that of *Brachidinium* lacking the extensions, maintaining the distinctive apical process, the prominent round to oval nucleus located in the left hyposome and the yellow-green pigmentation. The cell outline of the "standard" *K. papilionacea* showed a butterfly (Figs 4A-C) or Mexican-hat shape (Figs 4D-F). As reported in the cultures, in the present study large specimens (>40 µm wide) of *K. papilionacea* co-occurred with the smaller ones (Figs 4G, H). Other specimens with an elongate ellipsoidal shape and an apex that varied greatly from a pointed process to a prominent overhanging apical process could not be strictly assigned to *K. papilionacea* (Figs 4I, J). One of these specimens showed a nucleus that occupied most of the hyposome (Fig. 4I).

Brachidinium capitatum

A total of 29 specimens of *B. capitatum* were observed. The width at the cingulum level ranged from 20 to 62 µm with an average value of 39.1 ± 11.5 µm (Fig. 2B). The largest dimension of *Brachidinium* ranged from 65 to 130 µm with an average value of 98.4 ± 27.1 µm.

All the specimens of *Brachidinium* appeared in the

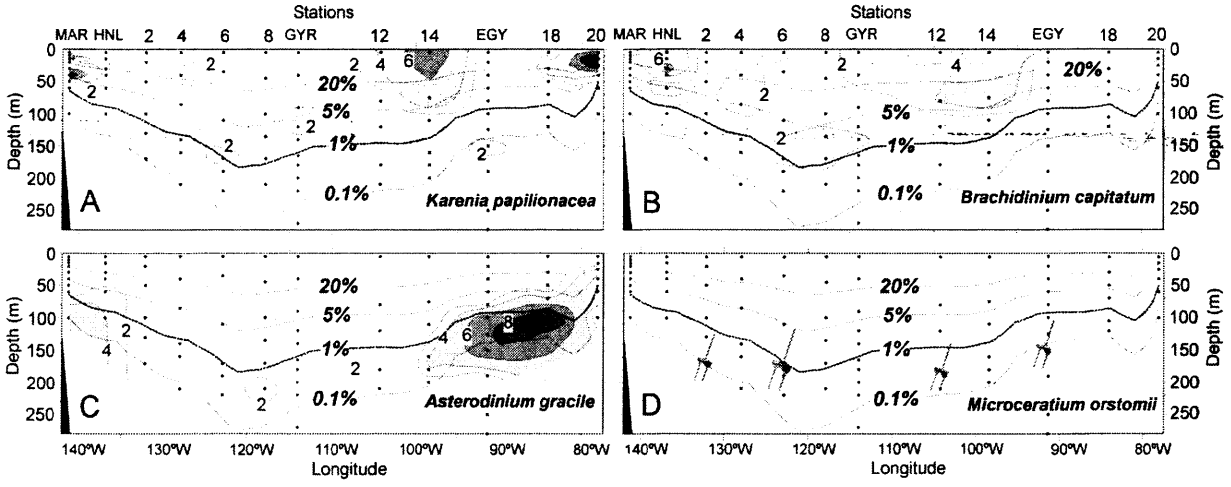

Fig. 3. Section plots of the distribution of A. *Karenia papilionacea*, B. *Brachidinium capitatum*, C. *Asterodinium gracile* and D. *Microceratium orstomii*. Abundance expressed as cells L^{-1}. The dashed lines represent the percentage of the surface irradiance.

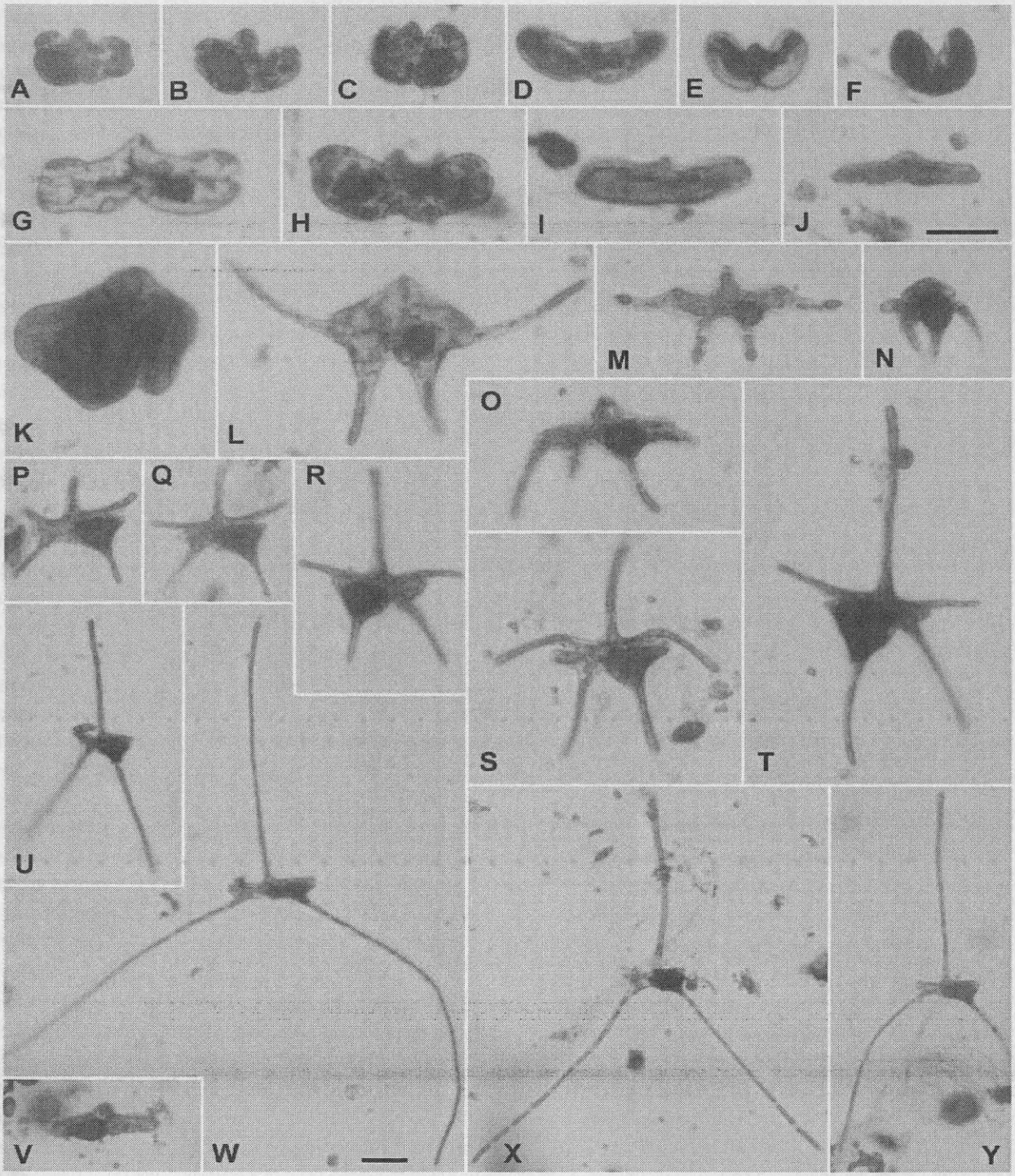

Fig. 4. Photomicrographs of brachidiniacean-*Karenia*, bright field optics. A-C. Butterfly-shaped *Karenia papilionacea*, D-F. Mexican hat-shaped *K. papilionacea*, G-H. Large cells of *K. papilionacea*, I-J. Unidentified ellipsoidal *Karenia* (note the large nucleus in Fig. 4I), K. Unidentified *Karenia* with the conical episome, L. Unidentified *Brachidinium* with the conical episome, M. *Brachidinium capitatum*, N. Unidentified small *Brachidinium* with a round episome, O. *B. capitatum* with extensions of different size, P-T. Specimens of *Asterodinium* with variable degree of development of the extensions, U. W-Y, *Microceratium orstomii*, V. Unidentified *Karenia*-like cell occurring with Fig. 4W. Location (see Fig. 1) and depth of the records: A. HNL 40 m, B. St. 20 15 m, C. GYR 120 m, D. MAR 40 m, E. St. 14 5m, F. MAR 40 m, G. St. 14 5 m, H. MAR 15 m, I. EGY 150 m, J. St. 18 30 m, K. St. 20 60 m, L. EGY 75 m, M. GYR 5 m, N. MAR 20 m, O. St. 14 5 m, P. MAR 100 m, Q. HNL 60 m, R. EGY 150 m, S. St. 8 210 m, T. St. 20 60 m, U. EGY 150 m, V-W. St. 6 170 m, X. St. 2 170 m, Y. St. 12 180 m. All the photomicrographs at the same magnification, except the figures U-Y that are reduced by a factor of 1.6. Scale bars: 20 μm.

euphotic zone. Its vertical distribution was wider in open waters and shallower near the Marquesas Archipelago and the Perú-Chile Current. The deepest record occurred at 170 m depth in the clearest waters associated with the South Pacific Gyre. The highest abundance, 6 cells L^{-1}, was recorded at 30 m depth in the surrounding waters of the Marquesas Archipelago (Fig. 3B). The length of the extensions showed a high variability. Nearly all the specimens had four extensions of similar length that can be interpreted as a synchronic growth of the body extensions (Fig. 4M). Exceptionally one of the specimens showed two alternate extensions longer than the other ones (Fig. 4O). If a non-synchronic growth of the extensions is discarded, it can be speculated that *Brachidinium* transforms into *Asterodinium* by the retraction of two of the four antapical extensions and the projection of the apical process. Nearly all the specimens of *Brachidinium* showed the distinctive apical process with variable degree of development (Figs 4L-O). One large specimen showed a conical episome, lacking the apical process (Fig. 4L). The contour of its episome resembled that of unidentified *Karenia* specimens that often co-occurred (Fig. 4K). One of the specimens of *Brachidinium* showed the smallest dimensions observed with only 16 μm wide and one of the lateral extensions was incompletely developed. The shape of the episome, round and lacking the apical process (Fig. 4N), resembled that in *Karenia bicuneiformis*. Both species of *Karenia*, *K. papilionacea* and *K. bicuneiformis* are very close genetically and coincided in the main morphological characters (Haywood *et al.* 2004). Despite the shape and position of the nucleus is not usually conservative in some species of *Karenia*, the nucleus in *K. papilionacea*, *K. bicuneiformis*, *Asterodinium*, *Brachidinium* and *Microceratium* was invariably located in the left hyposome.

Asterodinium gracile

A total of 33 specimens of *Asterodinium gracile* were observed. The width at the cingulum level ranged from 17 to 28 μm with an average value of 22.2 ± 4 μm, showing less size variability than in *B. capitatum* and *K. papilionacea* (Fig. 2C). The largest dimension of *Asterodinium* ranged from 35 to 200 μm (85.3 ± 57.1 μm). Nearly all the specimens were collected below the euphotic zone with the deepest record at 210 m depth (St. 8, Fig. 4S), coinciding with clearest waters (Fig. 3C). None specimen appeared in surface waters and the vertical distribution of the records of *Asterodinium* was shallower in more eutrophic stations (Fig. 3C). Some of the shallower records of *A. gracile* coincided with the deeper records of *B. capitatum*. *Karenia papilionacea* and *A. gracile* did not usually co-occur in open waters, except a few records of elongated cells of *K. papilionacea* below the euphotic zone (Fig. 3A). The highest abundance of *A. gracile* was recorded at St. 18 with 10 cells L^{-1} at 100 m depth (Fig. 3C). The variable degree of development of the body extensions in *A. gracile* is shown in Figs 4P-T. In well-developed specimens, the right hyposome was reduced and the cell body contents were expanded into the adjacent body extensions. However, the left hyposome cannot be reduced due to containing the prominent nucleus (Fig. 4T).

Microceratium orstomii

Four *Asterodinium*-like specimens with only 3 extensions, intermediate between *Asterodinium* and *Brachidinium* in terms of body extensions, corresponded to the description of *M. orstomii* (Sournia 1972a). From the episome only arose the elongate apical process or central apical extension and from the hyposome arose 2 antapical extensions (Figs 4U, W-Y). The extensions of *Microceratium* tended to be longer than in the common 5-extensions *Asterodinium*. The width at the cingulum level of *Microceratium* with values between 20-25 μm was similar to that of *A. gracile*. Exceptionally one of the specimens reached 310 μm of total length and 40 μm wide at the cingulum level, being the largest brachidiniacean observed (Fig. 4W). This specimen co-occurred with one specimen of a large elongated unidentified *Karenia* (Fig. 4V). The specimens of *Microceratium* appeared at 150 m (Fig. 4U), 170 m (Figs 4W, X) and 180 m depth (Fig. 4Y; Fig. 3D).

DISCUSSION

Trends in the distribution of the brachidiniaceans-*Karenia papilionacea*

The type species of *Brachidinium* and the other species, *B. taylorii* and *B. brevipes*, were described from surface samples. The two species of *Asterodinium* and *Microceratium orstomii* were collected at 100 m and 75 m depth, respectively (Taylor 1963; Sournia 1972a, b). From the same location, Sournia (1972b) also illustrated *K. papilionacea* collected from surface waters. In the offshore waters of the NE Africa upwelling, Margalef (1975) found exceptionally high abundances (up 4000 cells L^{-1}) of *B. capitatum* in the upper 30 m depth. In the same region, Estrada (1976, 1978) reported up 10000 cells L^{-1} of *B. capitatum* coinciding with 20000 cells L^{-1} of flattened

Karenia brevis-like cells in offshore surface waters. Gómez (2003) and Gómez *et al.* (2005a, b) found *Brachidinium* and *Asterodinium* at an average depth of 35 and 85 m, respectively, in several regions of the NW and Equatorial Pacific Ocean. The same pattern was observed in the present study in the SE Pacific Ocean (Figs 3B, C).

Haywood *et al.* (2004) reported that the abundance of *K. papilionacea* was lower than 1000 cells L^{-1} in the late austral summer in the coasts of New Zealand. In the European Atlantic coasts *Karenia brevis*-like cells also appear in summer with abundances that never exceeded 1500 cells L^{-1} (Nézan 1998). Yeung *et al.* (2005) found *K. papilionacea*-like cells with an abundance of 10 cells L^{-1} in the pier of the Hong Kong University. In the present study in open waters, the higher abundances of *K. papilionacea*, 10 cells L^{-1}, were found in the more productive regions.

Adaptation to light availability

The brachidiniaceans and *Karenia* are characterized by an unusual yellow-green bright pigmentation. *Brachidinium* and *Karenia* were encountered in the surface and *Asterodinium* and *Microceratium* below the euphotic zone. The records below the euphotic zone and surface waters of tropical seas required highly versatile pigment composition to adapt to different light regimes. Most of dinoflagellates have chloroplasts that contain chlorophyll c_2 and peridinin as the major carotenoid. However, the chloroplasts of *Karenia* have chlorophylls $c_1 + c_2$ and fucoxanthin-derived carotenoid but lacks peridinin (Tangen and Bjornland 1981), originated from a haptophyte tertiary endosymbiosis in an ancestral peridinin-containing dinoflagellate (Yoon *et al.* 2002). *Karenia* brevis (Davis) G. Hansen *et* Moestrup, responsible of massive toxic blooms in the Gulf of México, is the best known species of the genus. This species has a robust photosynthetic capability and accumulation of diadinoxanthin and diatoxanthin depending of the irradiance with minor adjustments in chlorophyll *a* and fucoxanthin contents that facilitate acclimation to variable irradiance regimes (Evens *et al.* 2001). This pigment plasticity could explain that *Asterodinium* can survive near the nutricline below 200 m depth with less than 0.1% of the surface irradiance. The availability of nitrate near the nutricline also favored the pigment accumulation as observed in *Asterodinium* (Gómez 2003; Gómez *et al.* 2005b). In addition, the cell shape of *A. gracile* with a strongly flattened cell body and elongate extensions seems to be an adaptation to increase the cross-section in light limiting conditions. Other shade flora members such as *Ceratium platycorne* Daday have highly pigmented wide flattened extensions (Sournia 1982).

Size and shape changes

The high variability of the size of the extensions of the brachidiniaceans has been remarked since the early works. In the description of *Brachidinium*, Taylor (1963) reported "the species is interesting in that the cells appear to exhibit a structural adaptation to their environment, namely, the production of elongate processes ... in this connection it might also be noted the specimen ... in less dense water exhibited a greater elongation of processes". The number of extensions of *Microceratium* (3-extensions) was lower, but the length of each extension was longer than in the typical 5-extensions *Asterodinium* (Figs 4P-Y). In addition to the increase of the cross-section for the photosynthesis, the elongated extensions are supposed to be associated with a reduction of the sinking speed and consequently a reduction of the energy required maintaining the cell in the euphotic zone. The projection of body extensions has been considered as an adaptive strategy for warm water dinoflagellates under low turbulence conditions (Zirbel *et al.* 2000).

Although the cell size is often an important taxonomic character in dinoflagellates, it can be variable. This variability was especially notorious in cultures of *K. papilionacea* with a usual range of width of 18-32 μm, but also co-occurring with cells 65-90 μm wide (Haywood *et al.* 2004) that has been also observed in natural waters in the present study (Figs 4G, H). Haywood *et al.* (2004, p. 175) reported "small to large cells present in cultures that were not separated into size classes because of the intergradations between sizes and because the significance of the size classes cannot be addressed until the life cycle of these species is known." *Karenia papilionacea* is also characterized by fast changes of shape and in cultures the apical process contracts forward when the cells are stressed (Haywood *et al.* 2004, p. 170) as already illustrated Sournia (1972b, p. 157). The live cells of *Brachidinium* were able to move the body extensions (Léger 1971; Gómez *et al.* 2005a). *Karenia bicuneiformis* was also able to change its morphology and the pointed or bulbaceous antapical tips observed in natural waters disappeared and the cells are rounder in cultures (Haywood *et al.* 2004, p. 173).

According to Raven (1986) the reduced size of the "small" subpopulations of microalgae allows an optimization of photon capture and nutrient uptake, such

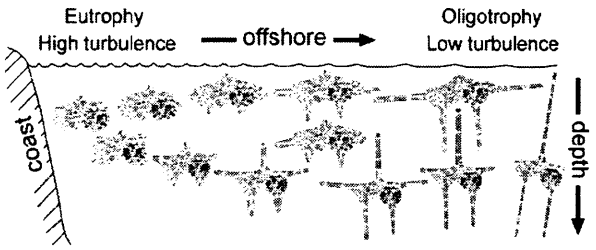

Fig. 5. Scheme of the distribution of the tentative life stages of *Brachidinium capitatum*.

that they may take optimal advantage of the conditions generally prevailing during the blooms (i.e., availability of nutrients, turbulence). In contrast, the "large" forms appeared to be more adapted for survival under non-bloom conditions (Raven, 1986). Consequently under the optimal conditions for growth such as cultures and eutrophic coastal waters, the smaller forms of *K. papilionacea* will predominate, whereas in open waters the projection of body extensions would constitute a competitive advantage (Fig. 5). Toxic species such as *Karenia* have been intensively investigated in high turbulence conditions such as cultures and coastal waters. Little is known on the adaptation of these species to the stratified open ocean.

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Observations on an H-shaped dinoflagellate. An example of the projection of body extensions in gymnodiniacean cells

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Running title: H-shaped dinoflagellate

Little is known about the morphological versatility of the unarmoured dinoflagellates. The morphology of the unarmoured dinoflagellate with a distinctive H-shaped contour is described from sub-surface waters of the Strait of Gibraltar (NE Atlantic) and the northern Philippine Sea (NW Pacific). The cell body was slightly hexagonal with two rounded-tip apical arms and two antapical sharp-pointed horns. A carina with a straight groove was located between the two apical arms. The cingulum was excavated, with a descending displacement of more than one-half body length and had an overhang. A round nucleus was located in the left hyposome. These forms may correspond to a gymnodiniacean cell that is able to project body extensions under unfavourable environmental conditions.

Key words: *Gyrodinium*, *Karenia*, dinoflagellate, Dinophyceae, phytoplankton, microalgae, Atlantic, Pacific

Introduction

During the routine microscopical analysis of several thousands of phytoplankton samples from the Atlantic, Mediterranean and Pacific waters, two similar specimens of an unknown distinctive dinoflagellate were observed. The present study describes the morphology of this interesting dinoflagellate from two distant geographical areas.

Materials and methods

Samples from the Atlantic Ocean were collected during a cruise aboard R/V *Thalassa* (2-9 September 1997) in the Strait of Gibraltar (Mediterranean Sea-Atlantic Ocean) (Fig. 1). Eight stations were visited and samples were collected at 9-11 depths at each station and 2.5 L seawater from Niskin bottles was filtered through 5-μm pore size mesh and the retained particles were carefully washed out, placed in glass bottles and preserved with acidified Lugol's solution. Sub-samples (10-100 ml) were allowed to settle for 24-48 h in Utermöhl chambers (GÓMEZ et al. 2000, GÓMEZ 2003). The specimen was photographed on an inverted microscope connected to a Leica Wild camera. The specimen showed the entire cell contents during the first microscopical observation. However, the cell body appeared empty after a re-examination several months later.

Samples from the Pacific Ocean were collected during a cruise aboard R/V *Soyo-Maru* (13-20 May 2002) in the Kuroshio Current and the northern Philippine Sea (Fig. 1). Seawater samples were collected using Niskin bottles at nine stations along the meridian 138°E from 28°0'N to 34°20'N, at 15 depths ranging between 5 to 200 m. Sample treatment and microscopical observations as in GÓMEZ et al. (2005).

Results

Two specimens of this highly distinctive dinoflagellate were observed from samples collected from Atlantic and Pacific waters (Gómez 2003, 2006; Gómez et al. 2005). The first specimen was collected in the Atlantic side of the Strait of Gibraltar at 65 m depth (2 September 1997; 35°58'N, 5°55'W; bottom depth 160 m). The phytoplankton assemblage was dominated by the diatom *Pseudo-nitzschia* spp. with a marked sub-superficial maximum at 40 m depth. The second specimen

was collected in the northern Philippine Sea at 150 m depth (16 May 2002; 30°N, 138°E; bottom depth 4050 m). The plankton assemblage at that depth was dominated by naked ciliates (<100 cells L^{-1}).

The maximal length of the H-shaped specimens was 52 and 55 μm and the width at the level of the cingulum was 25 and 27 μm for the Atlantic and Pacific specimens, respectively. The contour of the cell body in ventro-dorsal view was slightly hexagonal (Figs 2, 4, 6-8). The apex showed a carina or crest with a straight apical groove (Figs 7, 8). The excavated cingulum was descending and displaced by one-half of the body length and had an overhang (Fig. 6). The sulcus swung to the left before meeting the returning end of the cingulum. The intercingular region the cingulum and sulcus was Z-shaped (Figs 6, 7). A pore was observed near the beginning of the cingulum. This may correspond to a periflagellar pore where one or both flagella emerged (Fig. 6). The specimen was shaken until the transverse flagellum was separated from the cingulum (Fig. 9). The flagellum arose probably from the periflagellar pore showed in the figure 6. The nucleus was round and located in the left side of the hyposome (Figs 7, 8, 10).

The specimens showed four extensions of ~20 μm long radiating from the cell body. This resulted in the distinctive H-shaped contour (Fig. 4). Two curved flattened apical extensions with rounded-tips were projected from the episome (Fig. 14). The apical arms were in a different focal plane (Figs 6-8, 12-13). The right apical arm was more dorsally located than the left one (Figs 7, 8). The angle of the apical arms with respect to the episome was variable because the junctions were flexible (Figs 2, 4, 6-7). The two antapical extensions were straight and with acute ends. The left horn formed a right angle with the basis of the hyposome, whereas the right horn slightly diverged (Fig. 7).

In left lateral view, the cells showed an elongate bi-conical contour with the episome smaller than hyposome (Figs 3, 5, 10). The round nucleus was visible in lateral view as a pale region (Figs 10, 11). The Pacific specimen, observed in a better stage of conservation, showed a green pigmentation. Although, it was not discernible the presence of chloroplasts (Figs 6-8).

Discussion

No tabulation neither apical pore was observed. The forms of this study correspond to an unarmoured dinoflagellate (Figs 15-17). The groove along the carina reminds the straight apical groove that can be found in species belonging to the genera *Brachidinium* F.J.R. Taylor, *Asterodinium* Sournia, *Microceratium* Sournia and *Karenia* G. Hansen *et* Moestrup (GÓMEZ et al. 2005, GÓMEZ 2006). Flexible arms with rounded tips can be found in gymnodiniaceans such as *Brachidinium* or *Asterodinium* (GÓMEZ et al. 2005). However, the brachidiniaceans are strongly dorso-ventral flattened cells with a fucoxanthine-derived pigmentation. The forms of the present study were slightly dorso-ventrally compressed and the pigmentation seems to be closer to a typical peridinine-containing dinoflagellate. The shape of the intercingular region, descending and with an overhand, is similar to numerous species described under the genus *Gyrodinium* Kofoid *et* Swezy.

The two apical arms and the two antapical horns are most distinctive characters of the specimens. The projection of body extensions has been described as a strategy for the reduction of sinking speed in thecate species such as *Ceratocorys horrida* Stein (ZIRBEL et al. 2000). Little is known about the morphological versatility of the unarmoured dinoflagellates. The two specimens of the present study were found near the bottom of the euphotic zone at each location and predominating phytoplankton post-bloom conditions. It is hypothesized that the H-shaped forms corresponded to a stage of a versatile dinoflagellate that is able to project body extensions under unfavourable environmental conditions.

Acknowledgements

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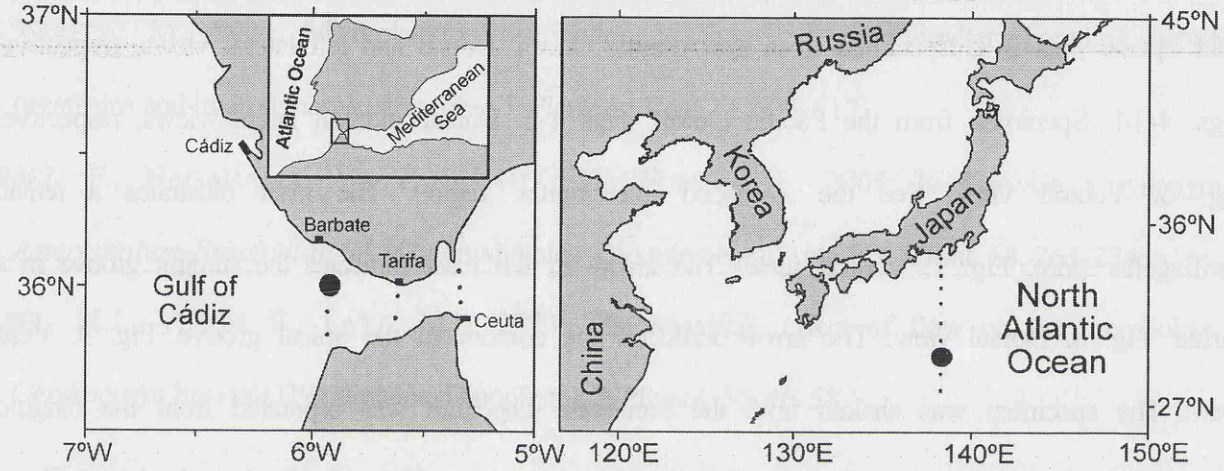
Figure captions

Fig. 1. Map of the stations occupied in the Atlantic and Pacific Oceans (full circles). Larger circles indicate the locations of the two records of the H-shaped dinoflagellate.

Figs 2-14. Photomicrographs of the H-shaped dinoflagellate, non-reversed images in bright field optics. Figs 2-3. Specimen from the Atlantic Ocean. Dorsal and left lateral views, respectively. Figs. 4-14. Specimen from the Pacific Ocean. Figs 4-5. Dorsal and left lateral views, respectively. Fig. 6. Ventral view. See the Z-shaped intercingular region. The inset illustrates a tentative periflagellar pore. Fig. 7. Ventral view. The arrow in the inset indicates the straight groove in the carina. Fig. 8. Dorsal view. The arrow indicates the contour of the apical groove. Fig. 9. Ventral view. The specimen was shaken until the transverse flagellum was separated from the cingulum. Figs 10-11. Left latero-ventral view. See the round nucleus. Figs 12-13. Apical views. Fig. 14. Detail of the tips of the apical extensions. N=nucleus; TF=transverse flagellum. The black spot in the photographs is not related to the cell. Scale bars = 20 μm.

Figs 15-17. Line drawings of the H-shaped dinoflagellate. Ventral, dorsal and left lateral view, respectively. Scale bar = 20 μm.


37°N
36°N
7°W
6°W
5°W
Atlantic Ocean
Mediterranean Sea
Cádiz
Barbate
Tarifa
Ceuta
Gulf of Cádiz
Russia
Korea
Japan
China
North Atlantic Ocean
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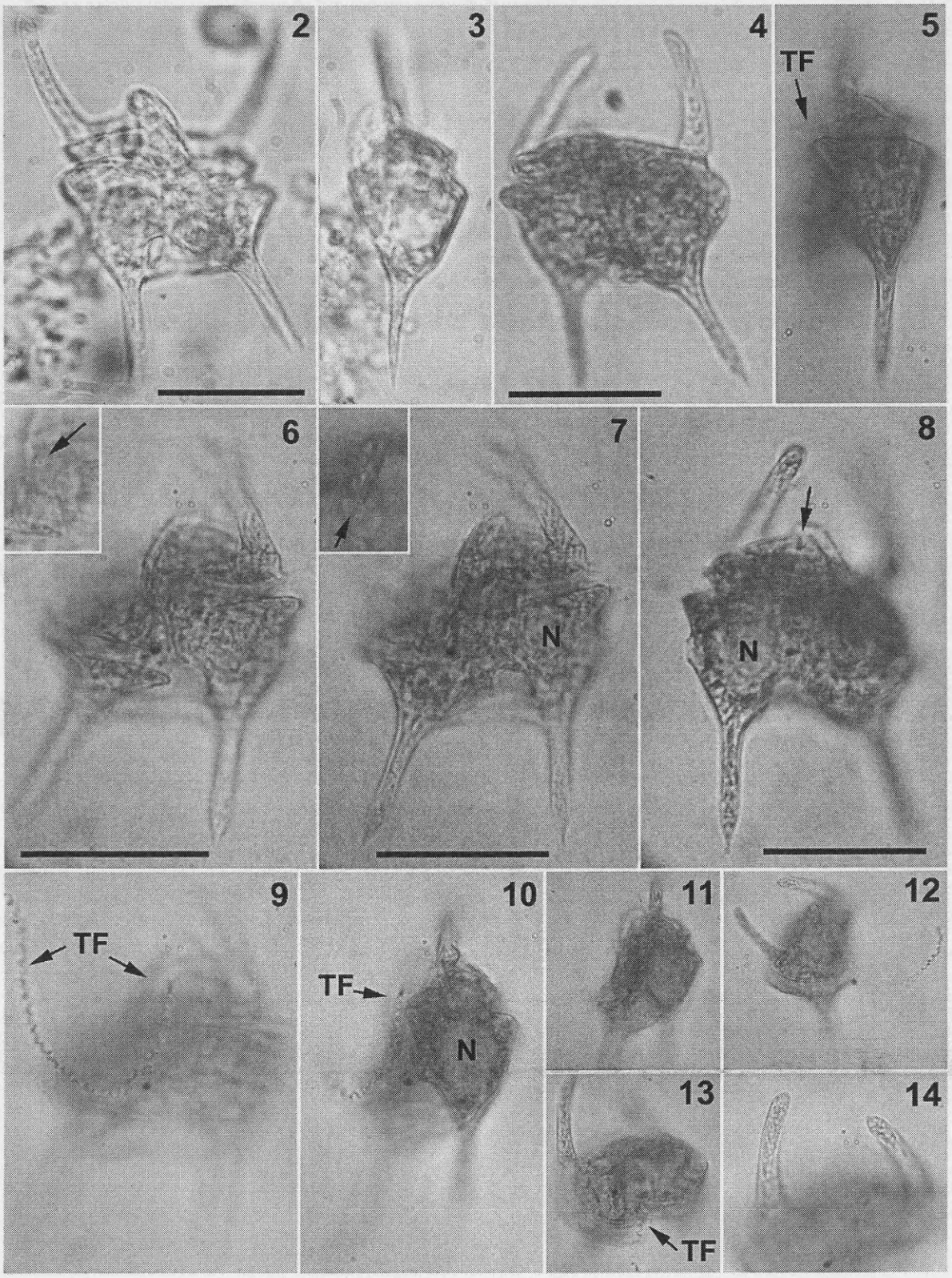
36°N
27°N
120°E
130°E
140°E
150°E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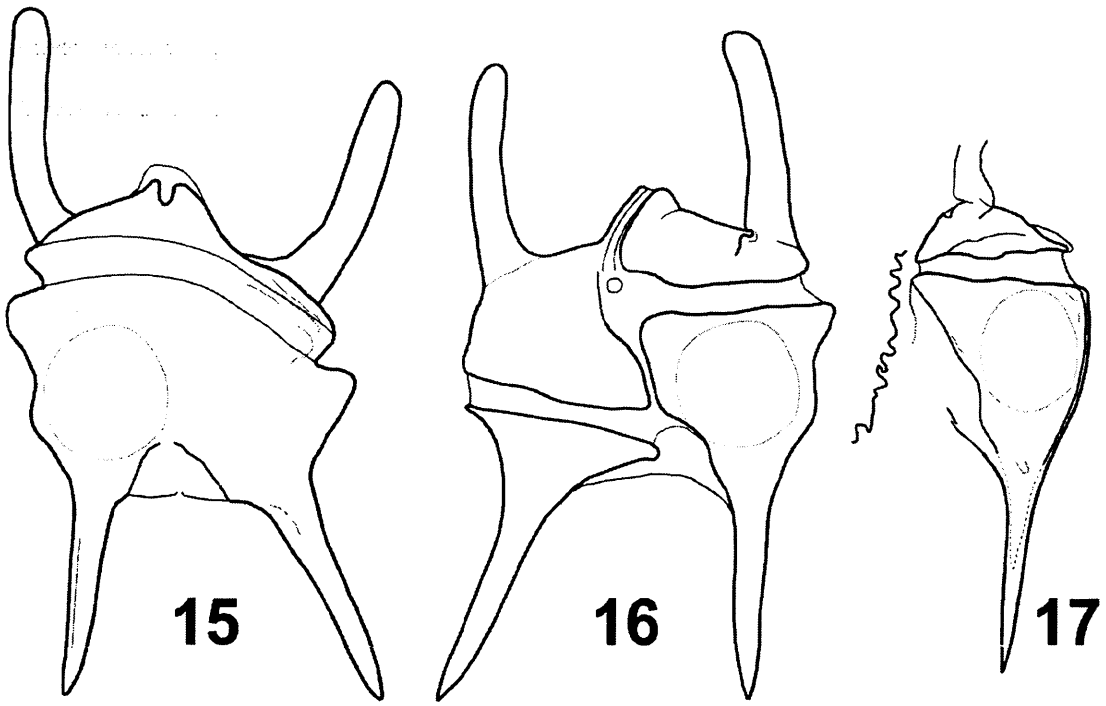
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16
17

3.2. Taxonomía y distribución de dinoflagelados poco conocidos:

3.2.2. *Ceratoperidinium*

Gómez, F. & Abboud-Abi Saab, M., 2003. Records of *Ceratoperidinium* Margalef (Dinophyceae) from the Mediterranean Sea. *Vie et Milieu* 53, 43-46.

Gómez, F., Nagahama, Y., Fukuyo, Y. & Furuya, K., 2004. Observations on *Ceratoperidinium* (Dinophyceae). *Phycologia* 43, 416-421.

VIE MILIEU, 2003, 53 (1) : 43-46

RECORDS OF *CERATOPERIDINIUM* MARGALEF (DINOPHYCEAE) FROM THE MEDITERRANEAN SEA

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CERATOPERIDINIUM
DINOFLAGELLATE
DINOPHYCEAE
PHYTOPLANKTON
MEDITERRANEAN SEA

ABSTRACT. – Records of dinoflagellates of the rare genus *Ceratoperidinium* Margalef *ex* Loeblich III are reported from the Mediterranean Sea. *C. yeye* Margalef was collected from the Bay of Palma de Mallorca (Balearic Is.) and *C.* cf. *yeye* from the Alborán Sea. From the Lebanese coastal waters, *C. yeye* was also reported and *C. mediterraneum* Abboud-Abi Saab. Other taxon, *Ceratoperidinium* sp., characterised by a distinct elongate apical process, is reported from the Bay of Palma de Mallorca. These species were collected from neritic and epipelagic waters and usually associated with phytoplankton post-bloom conditions.

CERATOPERIDINIUM
DINOFLAGELLÉ
DINOPHYCEAE
PHYTOPLANCTON
MER MÉDITERRANÉE

RÉSUMÉ. – Des données sur un genre rare de Dinoflagellé *Ceratoperidinium* Margalef *ex* Loeblich III de Méditerranée sont exposées. *C. yeye* Margalef a été trouvé dans la Mer d'Alborán et la Baie de Palma de Mallorca (Iles Baléares). Dans les eaux côtières libanaises, C. *yeye* et *C. mediterraneum* Abboud-Abi Saab ont aussi été recoltés. *Ceratoperidinium sp.*, caractérisé par un prolongement apical distinct, a été signalé dans la Baie de Palma de Majorque. Ces espèces ont été collectées dans des eaux néritiques, épipélagiques et souvent associées aux conditions d'un post-bloom de phytoplancton.

Dinoflagellates are well represented in the oligotrophic waters of the Mediterranean Sea. Despite the relative high number of studies performed in the Mediterranean Sea, some taxa are rarely reported and information on their ecology and distribution is scarce. This is the case for the species of the genus *Ceratoperidinium*.

The systematic position of this genus, which shape is reminiscent of peridinialeans and brachydiniaceans, remains uncertain. *Ceratoperidinium* has been considered as a thecate dinoflagellate of the order Peridiniales (Loeblich III 1982, Sournia 1986), but thecal plates have not been observed. According to Fensome *et al.* (1993), the rigid wall may be evidence of a pellicle. These authors placed this genus in the Ptychodiscales as an athecate dinoflagellate.

Ceratoperidinium yeye Margalef *ex* Loeblich III

The type species of the genus *Ceratoperidinium* was described from one individual in the Spanish Mediterranean coastal waters (Margalef 1969). The species presented a total length of 184 µm (63 µm excluding the antapical appendices) and a transversal diameter of 50 µm (Fig. 1A). This taxon was re-described as *Ceratoperidinium margalefii* by Loeblich III (1980) due to the lack of Latin diagnosis.

Later, Abboud-Abi Saab (1989) reported one specimen of *C. yeye* found in November 1988 at 5 m depth in the Lebanese coastal waters (33° 57' 34''N, 35° 35' 47''E). The Lugol fixed specimen was collected from waters with a temperature of 22°C, salinity 39.53, nitrate 0.26 µM and phosphate 0.04 µM. Mainly diatoms composed the surrounding phytoplankton assemblage, reaching an abundance of 6.1 cells ml^{-1} and dinoflagellates (mainly athecate forms) reaching an abundance of 3 cells ml^{-1}. The total length of the specimen was 236 µm, 67 µm excluding the appendices and the transdiameter was 59 µm. The cell size excluding the antapical appendices represented 25% of the total length. This specimen presented differences with the type species such as bigger size and protuberances that started at the 1/3 from the proximal

part, distributed regularly towards the tips of the antapical appendices (Fig. 1B).

Velásquez (1997) reported two records of *C. yeye* in the Gulf of Lions (NW Mediterranean Sea) in February 1988.

During a survey carried out in September 1999, one specimen that resembles *C. yeye* was observed at 20 m depth in the NW Alborán Sea (36°05'N, 05°12'W) from Lugol fixed water samples (Fig. 1D). Temperature was 17.3°C, salinity 36.77, nitrate 0.15 µM and phosphate 0.03 µM. The microphytoplankton assemblage was dominated by diatoms that reached an abundance of 7.7 cells ml^{-1}, mainly *Dactyliosolen fragilissimus*, *Leptocylindrus danicus*, *L. minimus* and *Pseudo-nitzschia* spp, whereas dinoflagellates reached an abundance of 2.6 cells ml^{-1} dominated by *Gymnodinium catenatum*. The observed phytoplankton assemblage corresponded to post-bloom conditions, in contrast with an assemblage dominated by *Chaetoceros curvisetus* more typical under the eutrophic conditions in this area (Gómez *et al.* 2000).

No size measurements of this specimen were performed. Cell size excluding the antapical appendices represented 29% of the total size whereas in the Margalef's figure this ratio was 34%. The antapical appendices were thicker than those

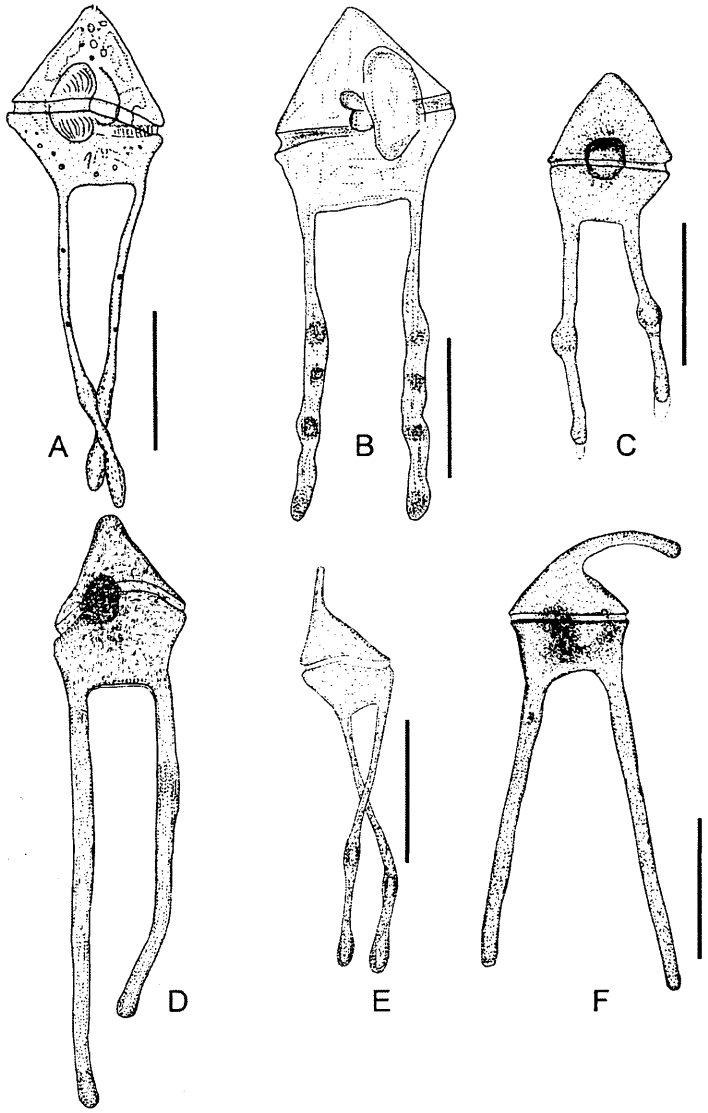

Fig. 1. – Line drawings of the records of *Ceratoperidinium* spp in the Mediterranean Sea. A, The type species, *Ceratoperidinium yeye* Margalef, adapted from Margalef (1969). B, *C. yeye* from the Lebanese coastal waters. C, *C. yeye* collected from the Bay of Palma de Mallorca (Balearic Is.). D, *Ceratoperidinium* cf. *yeye* recorded from the NW Alborán Sea. E, *Ceratoperidinium mediterraneum* Abboud-Abi Saab from the Lebanese coastal waters. F, *Ceratoperidinium* sp. collected from the Bay of Palma de Mallorca. Scale bar: 50 µm.

shown in Margalef (1969) and protuberances were not observed along the appendices.

In October 2001, a specimen of *C. yeye* was observed at 10 m depth in the Bay of Palma de Mallorca (Balearic Is.) (39°32'N, 2°36.3'E) from Lugol fixed water samples. The cell was 131 µm long (51 µm excluding the appendices) and the transdiameter was 42 µm (Fig. 1C). The antapical appendices were also thicker than those in Margalef's drawing and both of them presented clear protuberances in the middle of the appendices.

Ceratoperidinium mediterraneum Abboud-Abi Saab

Abboud-Abi Saab (1989) described this species from the Lebanese coastal waters from one specimen. The main characteristic of this taxon in comparison to *C. yeye* is the presence of a tip-rounded tubular apical (capitate) process (Fig. 1E). The total length was 134 µm, 46 µm excluding the appendices and the cingulum was 42 µm width (cell size excluding the antapical appendices represented 34% of the total size). The type species was found in July 1982 at 5 m depth in a coastal station (34°00'50''N, 35°30'40''E). The temperature was 27.2°C, salinity 39.2, nitrate 0.11 µM and phosphate 0.03 µM. The phytoplankton assemblage corresponded to spring post-bloom conditions dominated by diatoms (mainly *Dactyliosolen fragilissimus*) reaching an abundance of 23.6 cells ml^{-1} whereas the abundance of dinoflagellates was low (0.32 cells ml^{-1}). In October 1988, at the same station and the same depth, another specimen was collected with a total length of 137 µm (55 µm excluding the appendices) and the cingulum was 47 µm width. Cell size excluding the antapical appendices represented 40% of the total size. This specimen was collected from waters with a temperature of 26.6°C and a salinity of 39.3.

Ceratoperidinium sp

In November 2001, one specimen of the genus *Ceratoperidinium* was collected in the Bay of Palma de Mallorca (Balearic Is.) at 10 m depth. The cingulum diameter was 39 µm width and 112 µm of total length (including antapical and apical appendices) (Fig. 1F). This taxon presented a distinctive curved apical process more elongate than that of *C. mediterraneum*. In *Ceratoperidinium* sp. the antapical appendices were thicker than those in *C. yeye* and *C. mediterraneum* and protuberances along the antapical appendices were not observed. These characteristics resemble the antiapical appendices of the specimen *C.* cf. *yeye*, collected from the Alborán Sea. Based on the

Table I. – Records of *Ceratoperidinium* spp, including historical records.

Location (depth)	#	Date	Reference
C. yeye			
Castellón coast (10 m)	1	Aug., 1967	Margalef, 1969
Lebanese coast (5 m)	1	Nov., 1988	Abboud-Abi Saab, 1989
Gulf of Lions	2	Feb., 1988	Velásquez, 1997
Mallorca Bay (10 m)	1	Oct., 2001	This study
C. cf. *yeye*			
NW Alborán Sea (20 m)	1	Sept., 1999	This study
C. mediterraneum			
Lebanese coast (5 m)	2	Jul., 1982, Oct., 1988	Abboud-Abi Saab, 1989
Ceratoperidinium sp			
Mallorca Bay (10 m)	1	Nov., 2001	This study

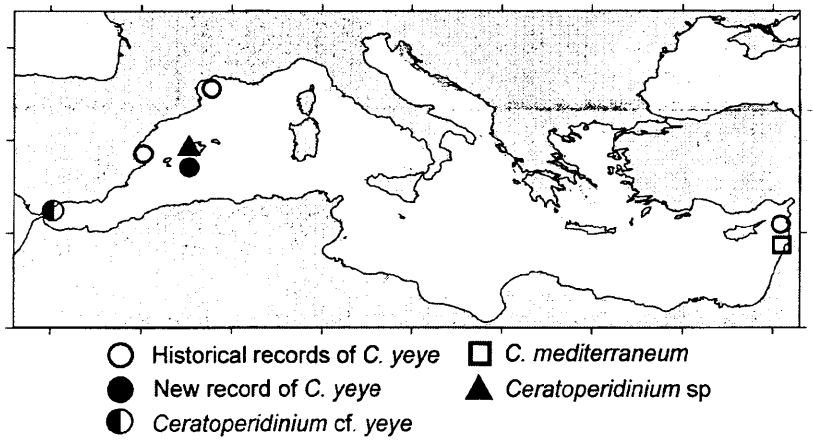

Fig. 2. – Location of the records of *Ceratoperidinium* spp.

length of the apical process, *C. mediterraneum* appears as an intergraded taxon between *C. yeye* and *Ceratoperidinium* sp.

Final remarks

As general trend, *C. yeye*, *C. mediterraneum* and *Ceratoperidinium* sp. seem to appear in coastal waters, being preferentially recorded from surface waters and usually associated with phytoplankton post-bloom conditions. Most of the specimens were collected under thermophilic conditions (summer-autumn), however the records by Velásquez (1997) in the Gulf of Lions in winter prevent us to considering *Ceratoperidinium* as a strictly warm-waters genus.

According to the available knowledge on the geographical distribution of *Ceratoperidinium*, these species can be considered as an exclusively Mediterranean taxa (Table I, Fig. 2). Despite the distinctive morphology, relative large size and being preferentially found in the surface coastal waters (more intensely studied), the records of these taxa are extremely low.

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RESEARCH NOTE

Observations on *Ceratoperidinium* (Dinophyceae)

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Until now, the rare dinoflagellate genus *Ceratoperidinium* Margalef has been recorded only from the Mediterranean Sea. For the first time, photomicrographs (bright field, Nomarski and epifluorescence) are reported from Lugol-fixed samples collected from the Sulu and Celebes Seas and the western Equatorial Pacific Ocean. The specimens showed high variability in the relative size of the flexible extensions. Several specimens corresponded to the type species, *Ceratoperidinium yeye*, and lacked the apical extension. Other specimens showed an apical extension of variable size that corresponded to the description of *C. mediterraneaum*. This taxon is considered to be a morphological variety of *C. yeye* on the basis of the high interspecimen variability in the length of the extensions; specimens intermediate between *C. yeye* and *C. mediterraneaum* occur where both forms coexist. The ventral view is proposed (confirmed by 4,6-diamidino-2-phenylindole staining) to be that with the nucleus located in the left side of the cell. Thecal plates were not observed in specimens stained with Fluorescent Brightener 28. Consequently, the placement of this genus in the order Peridiniales on the basis of the initial description from a single cell should be reconsidered.

Ceratoperidinium Margalef is a genus of planktonic marine dinoflagellate rarely reported in the literature. Margalef (1969) described the type species *Ceratoperidinium yeye* Margalef from a single individual collected in coastal waters of the Spanish Mediterranean Sea. Margalef reported a cell body that was pentagonal in outline and compressed dorsoventrally. The cingulum was weakly impressed and a sulcus was not observed. The cell surface was rigid and lacked sculpture or relief. No thecal plates were observed. The hypotheca (hyposoma) was drawn out into two long, slightly curved, rigid, cylindrical appendices with a row of three swellings at their extremities. The tips of the antapical extensions presented a tentacle-like shape. One large pusule, plastids and small drops of lipid occur in the cytoplasm and the nucleus is centrally located. Later, Loeblich (1982, p. 108) and Sournia (1986, p. 96) translated the description by Margalef (1969) to English and French, respectively.

The type species was redescribed as *C. margalefii* by Loeblich (1980) because of the absence of a Latin diagnosis. As reported by Sournia (1982, p. 153), Loeblich only added the Latin diagnosis, but instead of retaining the name with a new authority, *C. yeye* Margalef *ex* Loeblich III, he proposed the new name *C. margalefii* Loeblich III. The case of *C. yeye* is comparable to that of taxa such as *Petalodinium porcelio* J. Cachon & M. Cachon, in which the original publication of the type species lacked the Latin diagnosis; under the International Code of Botanical Nomenclature (Greuter *et al.* 2000; article 45.5 ex. 5), the name should retain its original authorship and date.

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After the initial record by Margalef (1969), Abboud-Abi Saab (1989) reported one specimen of *C. yeye* from Lebanese coastal waters. She further reported a new species, *C. mediterraneum* Abboud-Abi Saab (Abboud-Abi Saab 1989), that differs from the type species by the presence of a rounded tubular apical (capitate) process. The description of *C. mediterraneum* lacked a Latin diagnosis, line drawings and good-quality illustrations. This almost inaccessible publication goes unnoticed in or omitted from later literature.

Velásquez (1997) reported *C. yeye* in the Gulf of Lions (NW Mediterranean Sea) and more recently Gómez & Abboud-Abi Saab (2003) reported new records of *C. yeye* from the Alborán and Balearic Seas. These authors also reported a *Ceratoperidinium* sp. with a distinctive curved apical process more elongate than that in *C. mediterraneum* (Gómez & Abboud-Abi Saab 2003). There are no other records, either for the Mediterranean Sea (Gómez 2003) or for the rest of the world, to the best of our knowledge.

Ceratoperidinium has been placed in the family Ceratoperidiniaceae Margalef (Loeblich 1982) or *incertae sedis* (Sournia 1986), both in the order Peridiniales Haeckel, and later tentatively as an unarmoured taxon of the order Ptychodiscales Fensome, Taylor, Norris, Sarjeant, Wharton & Williams (Fensome *et al.* 1993).

This study presents photographic records of the genus for the first time. We tried to elucidate the presence of cellulose thecal plates by using the Fluorescent Brightener staining technique. The position and the shape of the nucleus were studied by using a DNA fluorochrome. The orientation of the cell is proposed for the first time. The morphological variability in the relative size of the extensions is emphasized.

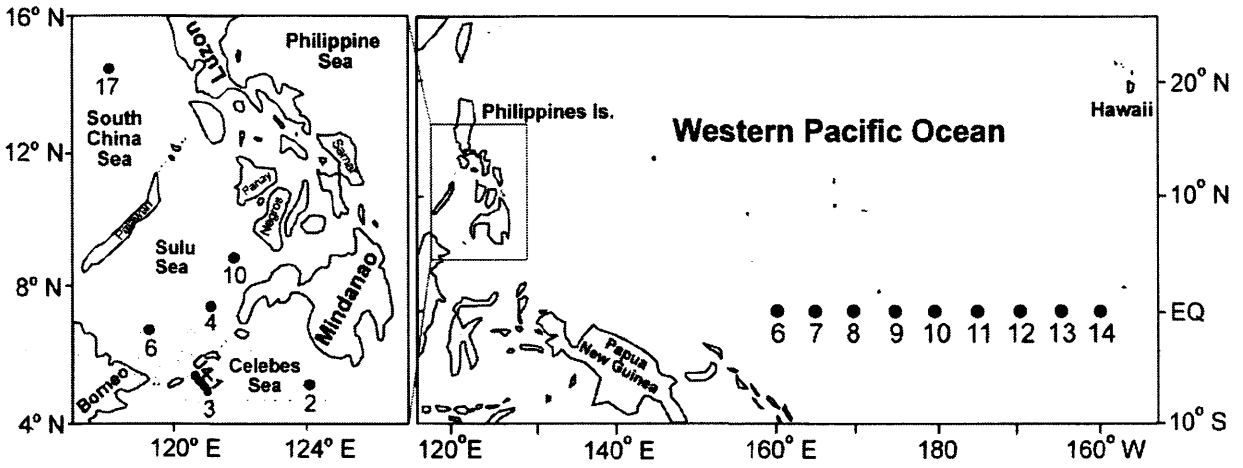


Fig. 1. Locations of the sampling stations in the tropical and western Equatorial Pacific Ocean.

Specimens were collected during two cruises: (1) aboard R/V Hakuho-maru (7 November–18 December 2002) in the Celebes, Sulu and South China Seas (Fig. 1). Sea water samples were collected by using Niskin bottles in 10 stations at six discrete depths from 0 to 150 m; and (2) aboard R/V Mirai (15–28 January 2003) along the equator from 160°E to 160°W. Sea water samples were collected by using Niskin bottles in nine stations at 14 discrete depths from 5 to 200 m. Samples were preserved with acidified Lugol's solution (Hasle & Syvertsen 1997) and stored at about 5°C. Samples of 400 ml were concentrated by settling in glass cylinders; concentrates were left to settle in standard sedimentation chambers and examined in a Diaphot inverted microscope (Nikon, Tokyo, Japan) using bright field optics. Cells were photographed on an inverted light microscope connected to a Nikon digital camera (Coolpix 4500).

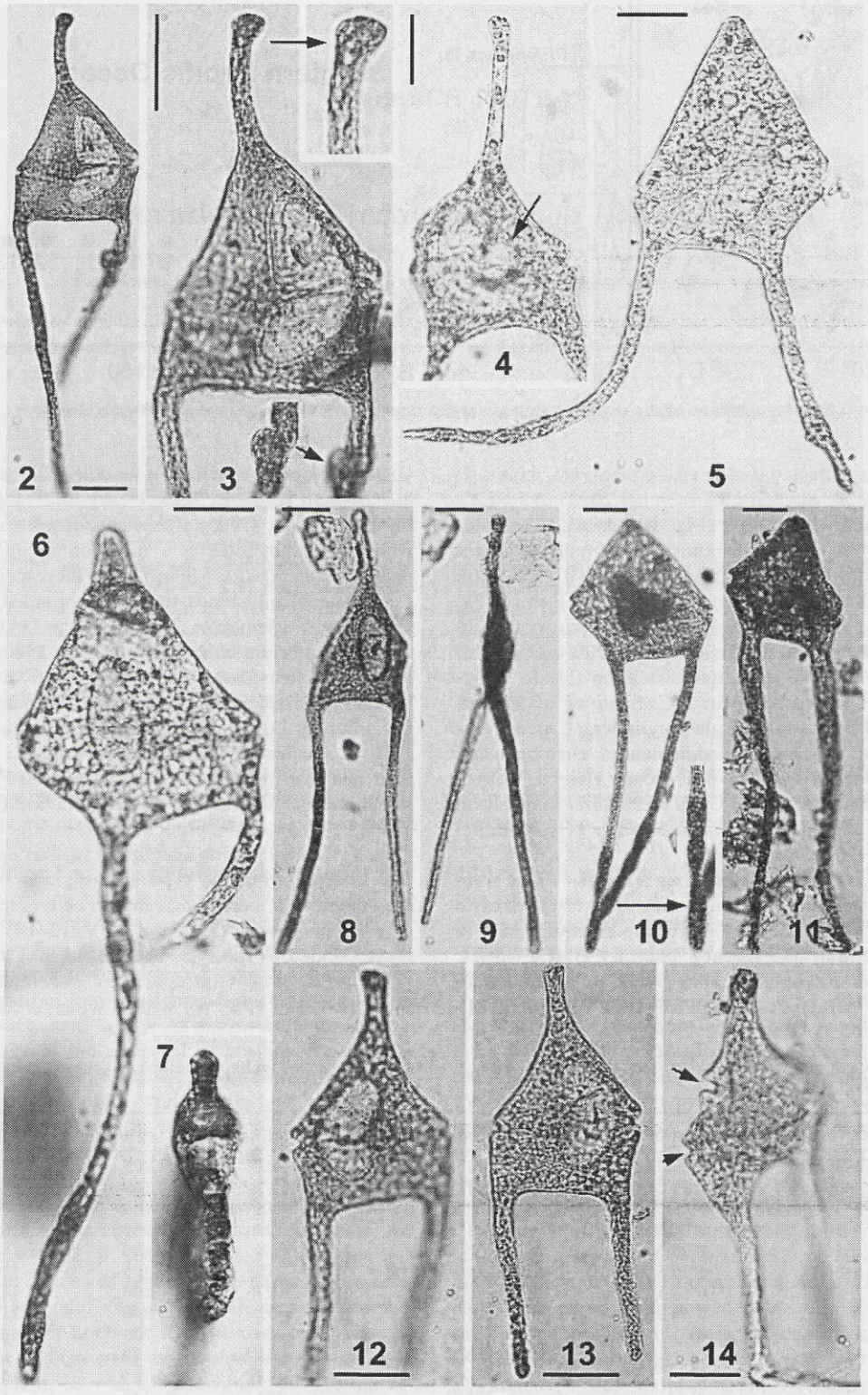
Several specimens were isolated using a capillary tube from the chambers, transferred to a glass slide and observed with an Olympus microscope (BX51; Tokyo, Japan) equipped with Nomarski differential interference contrast (DIC) optics. High-magnification microphotographs (×600 or ×1000) were obtained with an Olympus digital camera (C3040ZOOM). One specimen was stained by adding Fluorescent Brightener 28 (Sigma, St Louis, MO, USA) following the protocol of Fritz & Triemer (1985). Three specimens (one under division) were stained by adding a mix containing 4,6-diamidino-2-phenylindole (DAPI; Sigma) and Fluorescent Brightener. The DAPI specifically binds to double-stranded DNA, and when excited with ultraviolet (UV) light the DAPI–DNA complex fluoresces a bright blue (Porter & Feig 1980). Epifluorescence microscopy was done with Olympus (BX60) and Zeiss Axiophot2 microscopes (Zeiss, Jena, Germany) to excite with UV light for DAPI and Fluorescent Brightener stains.

Eight specimens were observed from the Sulu and Celebes Seas and five from the western Equatorial Pacific Ocean. The maximum occurrence was in the Sulu Sea (station 4; 7°25'N, 121°12.5'E), with four specimens (10 cells l^{-1}) at 30 m depth (Fig. 1; Table 1). Nine specimens had an apical protuberance that differed from the type species; they were closer to *C. mediterraneum*, here considered to be a morphological variety of the type species (Figs 2–4, 8, 9, 12–14). Three specimens corresponded to the type species, lacking the apical process (Figs 5, 10, 11). One specimen was intermediate between these two taxa (Fig. 6), with a wider section at the base of

Table 1. Stations, depth, geographic coordinates (latitude, longitude) and dimensions: W, width at the level of the cingulum; L, total length of each record of *Ceratoperidinium yeye*.

Station	Depth (m)	Latitude	Longitude	W (μm)	L (μm)	Figs
4	−30	7°25.3'N	121°12.5'E	43	205	2–3
4	−30	7°25.3'N	121°12.5'E	37	165	
4	−30	7°25.3'N	121°12.5'E	48	180	8–9, 18–20
4	−30	7°25.3'N	121°12.5'E	38	150	15
4	−50	7°25.3'N	121°12.5'E	38	180	
2	−30	5°10.8'N	124°04.9'E	39	105	12–13
6[1]	−30	6°54.1'N	119°11.1'E	37	100	14, 16–17, 21–24
6[2]	−20	6°54.1'N	119°11.1'E	52	200	11
6[2]	−60	0°	160°E	68	225	10
6	−100	0°	160°E	45	172	
8	−70	0°	170°E	48	185	4
9[2]	−120	0°	175°E	52	145	5
11[3]	−120	0°	175°W	65	230	6–7

[1] Specimen undergoing division.
[2] No apical process.
[3] Apical process scarcely developed.



Figs 2–14. *Ceratoperidinium yeye,* bright field optics. See Table 1 for location of the records and the size of the specimens. Scale bars = 20 μm.

Figs 2, 3. Ventral views of one specimen. The arrow in Fig. 3 indicates a knob on one of the antapical extensions, and the arrow in the inset the extremity of the apical process.

Fig. 4. Dorsal view of a specimen showing a hole (arrow).

Fig. 5. Ventral view of another specimen lacking the apical process.

Figs 6, 7. A specimen intermediate between *C. yeye* and the morphological variety *C. mediterraneum.* Fig. 7 shows a lateral view of the cell body with a wider section at the base of the short apical extension.

the apical tip seen in lateral view (Fig. 7). One of the specimens was observed under division, with two contours of groove observed in one side of the cells (Figs 14, 16, 17, 21–24). The size of the extensions relative to the cell body varied between the specimens (Figs 2–14). The antapical appendices were highly flexible. One of the specimens had a protuberance in one of the antapical appendices that we named 'the knob' (Fig. 3). As general trend, the antapical extension was slightly shorter in the side where the cingular groove was more apical (near the nucleus). From Lugol-fixed specimens, the maximum length ranged from 100 to 230 μm and the width at the cingulum level was 37–68 μm; specimens lacking the apical extension were larger than the others (Table 1). The cingulum was weakly impressed, and inclined relative to the base of the cell body. Neither flagellum nor sulcal groove was observed (Figs 18, 19). A slight irregularity, perhaps pores, appeared near the basis of the hyposoma (Fig. 20).

The DAPI staining reveals the nucleus to be kidney-shaped and located laterally, glowing brightly under UV excitation (Fig. 17); under light microscopy, it appears as a pale area (Fig. 22) and microfilaments (chromosomes) can sometimes be seen (Fig. 15).

Cellulose thecal plates were not observed in specimens stained with Fluorescent Brightener and a mixture of DAPI–Fluorescent Brightener illuminated with UV light. However, cellulose thecal plates were observed in cells of *Prorocentrum* added to the samples as a positive control. The same protocol has been successfully used previously with other thecate dinoflagellates.

Dinoflagellates have been divided into naked (or unarmoured) and thecate (or armoured). However, the distinction is not clear-cut (Dodge & Crawford 1970). The scarce information on our genus is based on the single record by Margalef (1969). The systematic position of this genus remains uncertain; the pentagonal shape of the cell body is reminiscent of peridinialeans, but the presence of extensions suggests the brachydiniaceans. Loeblich (1982, p. 108), based on Margalef (1969), reported 'the thecal tabulation is unknown; however, the presence of a large apical pore indicates that a thecal layer is present'. We have not observed any apical pore. Loeblich (1982) placed this genus in the family Ceratoperidiniaceae Margalef of the order Peridiniales. Sournia (1986, p. 96) placed *Ceratoperidinium* in an undetermined position – *incertae sedis* – in the order Peridiniales. Fensome *et al.* (1993) interpreted that the rigid wall that might be evidence of a pellicle and tentatively placed the genus as an athecate dinoflagellate of the order Ptychodiscales. According to Fensome *et al.* (1993, p. 54) the ptychodiscacean cell wall tends to be very flexible, due to the presence of a well-developed pellicle with cellulose as principal component (Morrill & Loeblich 1981). Fluorescent Brightener specifically stains cellulose, the main component of the dinoflagellate theca (Fritz & Triemer 1985). According to our results, *Ceratoperidinium* lacks the thecal plates that are characteristic of members of the order Peridiniales.

The orientation of the genus is unresolved. Neither flagellum nor sulcal groove was observed. The description by Margalef reported one large pusule and that the nucleus was located centrally (see also Loeblich 1982, p. 108). However, the use of DAPI staining in this study reveals that the nucleus is located laterally (Fig. 17) with microfilaments (chromosomes) visible under DIC microscopy (Fig. 15).

The cingulum is left-handed and weakly impressed (Figs 18–20). Observation at different focus levels reveals that a discontinuity in the cingulum occurs in the side opposite the nucleus (Fig. 19). We consider that this view, with the nucleus in the left side of the cell, is the ventral position (Figs 25, 26).

The specimens collected in the Pacific Ocean were very variable in the relative size of the antapical extensions (Figs 2–14). At the same stations were found specimens with and without an apical extension (Table 1). In the Mediterranean waters, Gómez & Abboud-Abi Saab (2003) reported the presence of *C. yeye* and *Ceratoperidinium* sp. (with an elongate and curved apical extension) at the same location. Consequently, *C. mediterraneum* was reported as intermediate between *C. yeye* and *Ceratoperidinium* sp. Athecate dinoflagellates such as *Pseliodinium vaubanii* Sournia are very variable with respect to the size of their flexible extensions (Sournia 1972). Recently, Konovalova (2003) reported that *P. vaubanii* constitutes one stage in the life history of *Gyrodinium falcatum* Kofoid & Swezy. Within this context, the relative size of the apical extension of *Ceratoperidinium* should not be considered as a criterion for the differentiation of species. Until further research, taxa such as *C. mediterraneum* or *Ceratoperidinium* sp. (Gómez & Abboud-Abi Saab 2003) should be considered as a morphological variety of the type species. Cell division occurs in specimens with short apical extensions. Specimens lacking the apical extension showed a larger size than those with the apical extension.

Despite the distinctive morphology and the relatively large size (> 200 μm), records of *Ceratoperidinium* are extremely rare. Even distinctive taxa remain insufficiently known, especially in open waters of the subtropical and tropical oceans.

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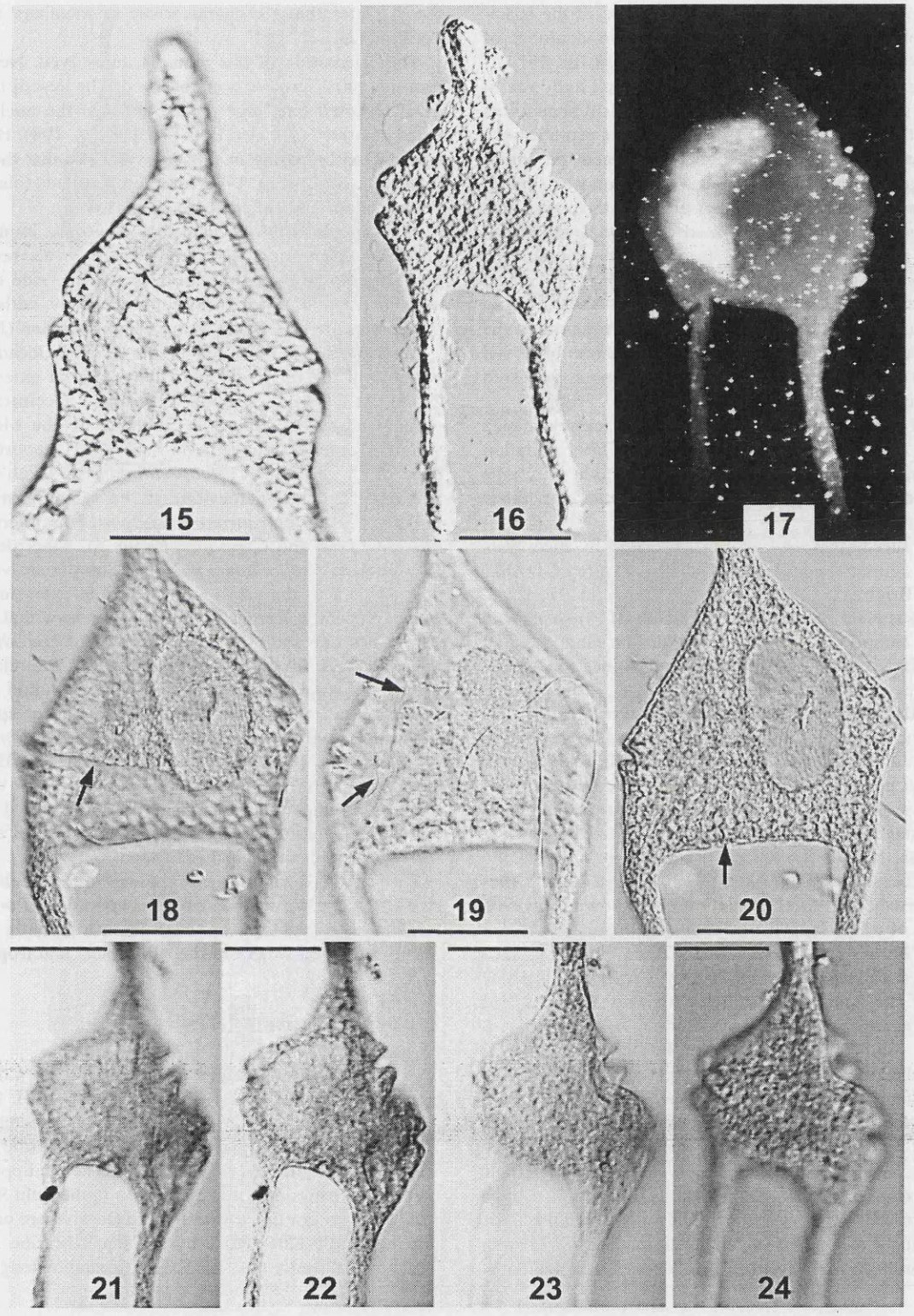
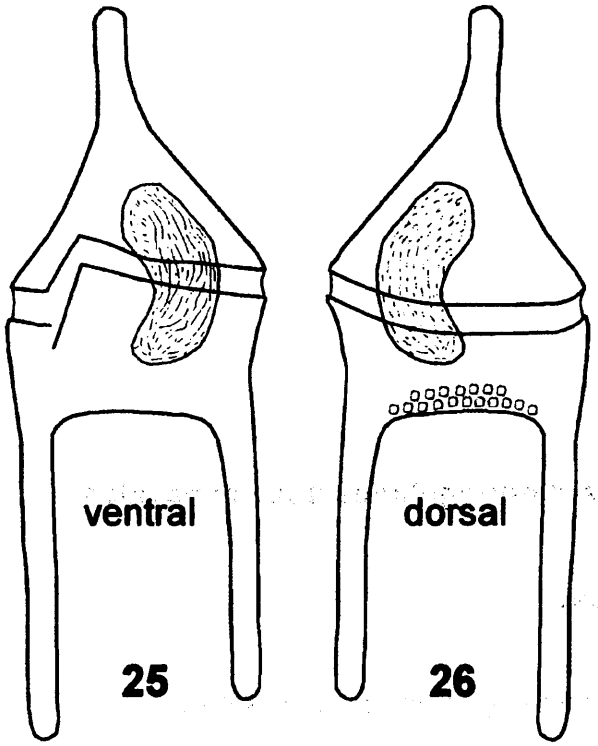
Figs 8, 9. Ventral and lateral views, respectively, of another specimen.
Figs 10, 11. Two different specimens lacking an apical extension; dorsal view. The arrow in Fig. 10 (inset) indicates the extremity of the antapical extension.
Figs 12, 13. Dorsal and ventral views, respectively, of the same specimen.
Fig. 14. Specimen undergoing division. The arrows indicate the cingular grooves.



Figs 15–24. *Ceratoperidinium yeye,* DIC (except Fig. 17, epifluorescence). Scale bars = 20 μm.
Fig. 15. Specimen in dorsal view showing microfilaments within the kidney-shaped nucleus.
Fig. 16. Specimen in dorsal view undergoing division.
Fig. 17. The DAPI-Fluorescent Brightener–stained specimen showing the nucleus glowing brightly in a lateral location under UV excitation. No Fluorescent Brightener–stained cellulose (blue) was observed that would indicate the presence of thecal plates.
Figs 18–20. Detail of the cingulum.
Fig. 18. Ventral view. The arrow indicates the cingulum.
Fig. 19. Ventral view. The arrows indicate the discontinuity in the cingular groove (the fibres are not related to the specimen).
Fig. 20. The arrow points to pores in the surface of the base of the hyposoma.
Figs 21–24. Specimen undergoing division. Note the shape of the nucleus in Fig. 22 (also Fig. 17).



Figs 25, 26. Schematic line drawings of the orientation (ventral and dorsal, respectively) of a *Ceratoperidinium* cell.

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3.2. Taxonomía y distribución de dinoflagelados poco conocidos:

3.2.3. *Gynogonadinium* gen. prov.

Gómez, F. *Gynogonadinium aequatoriale*, gen. et sp. nov. a new dinoflagellate from the open western Equatorial Pacific. *Algae*, enviado.

Gynogonadinium aequatoriale gen. *et* sp. nov., a new Dinoflagellate from the Open Western Equatorial Pacific

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Short running title: *Gynogonadinium aequatoriale* gen. *et* sp. nov.

A new genus and species of marine dinoflagellate from the open western equatorial Pacific Ocean, *Gynogonadinium aequatoriale* gen. *et* nov. sp., is described from light and scanning electron micrographs. This laterally compressed unarmoured taxon had a triangular cell body in lateral view with two different elongate extensions. The end of the apical extension was spherical with a groove that arises from the epicone in the ventral side of the cell. The antapical extension was longer. The dorsal part of the cingulum showed undulated lists in each margin. The nucleus was ellipsoidal and perpendicularly crossed the cingulum. Dimensions of cells were 90-110 μm long and 43-50 μm wide in lateral view at the level of the cingulum. *Gynogonadinium* is placed in the order Gymnodiniales, family uncertain.

Key Words: Dinophyceae, equatorial Pacific Ocean, *Gynogonadinium aequatoriale*, phytoplankton, taxonomy

INTRODUCTION

Taxonomic studies of unarmoured dinoflagellates from open waters of tropical oceans are few in number. The Western Pacific Warm Pool (western equatorial Pacific Ocean) is a poorly studied region of the world's oceans for phytoplankton taxonomy. From samples collected in that region under influence of the phenomenon of El Niño in 2003, several specimens of a distinctive unarmoured dinoflagellate, which could not be ascribed to any known genus, were found. Despite the scarce specimens available and its delicacy, by using the Takayama's method (Takayama 1985) was successfully obtained SEM pictures. This dinoflagellate with a distinctive shape and unique morphological characters is here described.

MATERIALS AND METHODS

A cruise was carried out on board *R/V Mirai* (15-28 January 2003) along the Equator from 160°E to 160°W. Samples were collected from 9 stations at 14 depths between 0 and 200 m depth. Samples were collected using Niskin bottles, preserved with acidified Lugol's solution and stored at 5°C. Subsamples (400 mL) were allowed to settle in glass sedimentation cylinders. The top 350 mL of each sample was siphoned off progressively over 5 days using a length of small-bore tubing. The remaining 50 mL was settled in composite sedimentation chambers. Light microscopy observations were made as described in Gómez *et al.* (2004). For scanning electron microscopy (SEM), specimens were isolated with a capillary from sedimentation chambers and adhered to poly-L-lysine-coated cover-slip. Fixed cells attached to the cover-slip were rinsed twice in distilled water for 5 min each. Cells were then dehydrated through an ethanol series, dried in a critical point drier (HCP-2, Hitachi, Tokyo, Japan), and coated with Au-Pd (Takayama 1985). Observations were made using a SEM (S-800, Hitachi, Tokyo, Japan).

RESULTS AND DISCUSSION

***Gynogonadinium aequatoriale* gen. *et* sp. nov.**

Figs. 1-14

Diagnosis: *Cellula laterale compressae, 90-110 μm longae et 43-55 μm latae. Media pars aequa portione a cingulo divisa. Hypoconus et epiconus triangulatus. Duo longa curvaque brachia tumescentibus extremitatibus, aliquid dissimilar. Cellula apertae femina gonada. Nucleus dinokaryoticus elongatus, in parte centralis cellulae situs.*

Cells of *Gynogonadinium aequatoriale* are laterally compressed, with size 90-110 μm in length 43-55 μm in width. The cingulum divides the cell in two similar parts. Hypocone and epicone are triangular in shape. Two curve extensions of different size arise from the extremes. The cell resembles the female gonad. The dinokarion is located in the part central of the cell.

Holotype: Figure 8 collected by F. Gómez.

Isotype: Figures 3-7.

Type locality: Western equatorial Pacific Ocean (0°, 160°E), 15 m depth.

Etymology: *Gyn-, Gyno-* (from Greek: female, woman); *Gonad-, Gonado-* (from Latin: ovary or testis based on Greek: *gonos*: "seed"): referring the contour of the cell that resembles the female gonad. *Aequator* (from Latin: equator): referring to the type locality.

Morphology: Based on light microscopy, the outline of the cell body in lateral view was triangular with two elongate extensions. The median cingulum was slightly deflected antapically on the dorsal side. The outline of the cell resembled a female gonad (Figs. 1, 3). One flexible, elongated apical extension arose from the ventral side of the cell body. The end of the apical extension was spherical with ~5 μm in diameter (Figs. 1-4). The antapical extension, also arising from the ventral side of the cell body, was longer than the apical extension. The ending of the antapical extension was roughly spatulate in shape (Fig. 5). The

nucleus was visible under differential interference contrast optics (Fig. 6) and, when stained with DAPI (4,6-diamidino-2-phenylindole), glowed brightly under UV excitation. In lateral view, the nucleus had an elongate ellipsoidal shape, perpendicularly crossing the median cingulum. The part of the nucleus located in the epicone was curved towards the ventral side (Figs. 5-7). The brownish pigmentation suggested the presence of peridinine. No chloroplasts were observed. Unfortunately from Lugol-preserved specimens cannot be tested the presence of the chlorophyll-*a* by epifluorescence microscopy.

One of the specimens was successfully prepared for SEM (Figs. 8-13). SEM allowed observing the sulcus, two flagellar pores (Fig. 12) and an apical groove from the epicone to the extreme of the apical extension (Figs. 10, 11). The groove surrounded the spherical-shaped end of the apical extension (Fig. 11). The margins of the cingulum in the dorsal side showed undulated lists, anterior and posterior (Fig. 13). The specimens ranged from 90-110 μm long and 43-55 μm wide at the cingulum level (Table 1).

Habitat: Seven specimens were collected from five consecutive sampling stations along 2200 km in the equator from 160ºE to 180º between 15 and 110 m depth. This study was a part of twelve cruises carried out in the open Pacific between 41°N and 34°S (Gómez 2005). The records of *Gynogonadinium aequatoriale* were restricted to the westernmost edge of the Equatorial Pacific Ocean (Table 1).

Species comparison: *Gynogonadinium* is laterally compressed taxon and consequently the ventral side is difficult to observe under light microscopy. If the ventral position is forced (Figs. 2, 4), the outline of this taxon could resemble *Gyrodinium falcatum* Kofoid *et* Swezy (=*Pseliodinium vaubanii* Sournia) (Kofoid 1931; Konovalova 2003). However, *Gynogonadinium* (Figs. 14-15) has a cell body of triangular contour in lateral view whereas *Gyrodinium falcatum* has an ellipsoidal shape in both lateral and dorso-ventral views. Other distinctive morphological characters such as the undulated cingular lists and the extensions are unique in *Gynogonadinium*. The cingular lists have been described in armoured

dinoflagellates (Almazán Becerril and Hernández-Becerril 2002; Vershinin and Morton 2005), but rarely in unarmoured dinoflagellates. Balech (1975, p. 11) illustrated cingular list in *Gymnodinium* cf. *diploconus* Schütt. The apical groove as found in *Gynogonadinium* is a morphological character of some gymnodiniaceans (Takayama 1985). I hesitate to assign this species to any currently known family, and until further research, *Gynogonadinium* is placed in the order Gymnodiniales, family uncertain.

ACKNOWLEDGEMENTS

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Table 1. *Gynogonadinium aequatoriale*: stations, depth, geographic coordinates (latitude, longitude), date and dimensions: W, width at the level of the cingulum in lateral view; L, total length of each record.

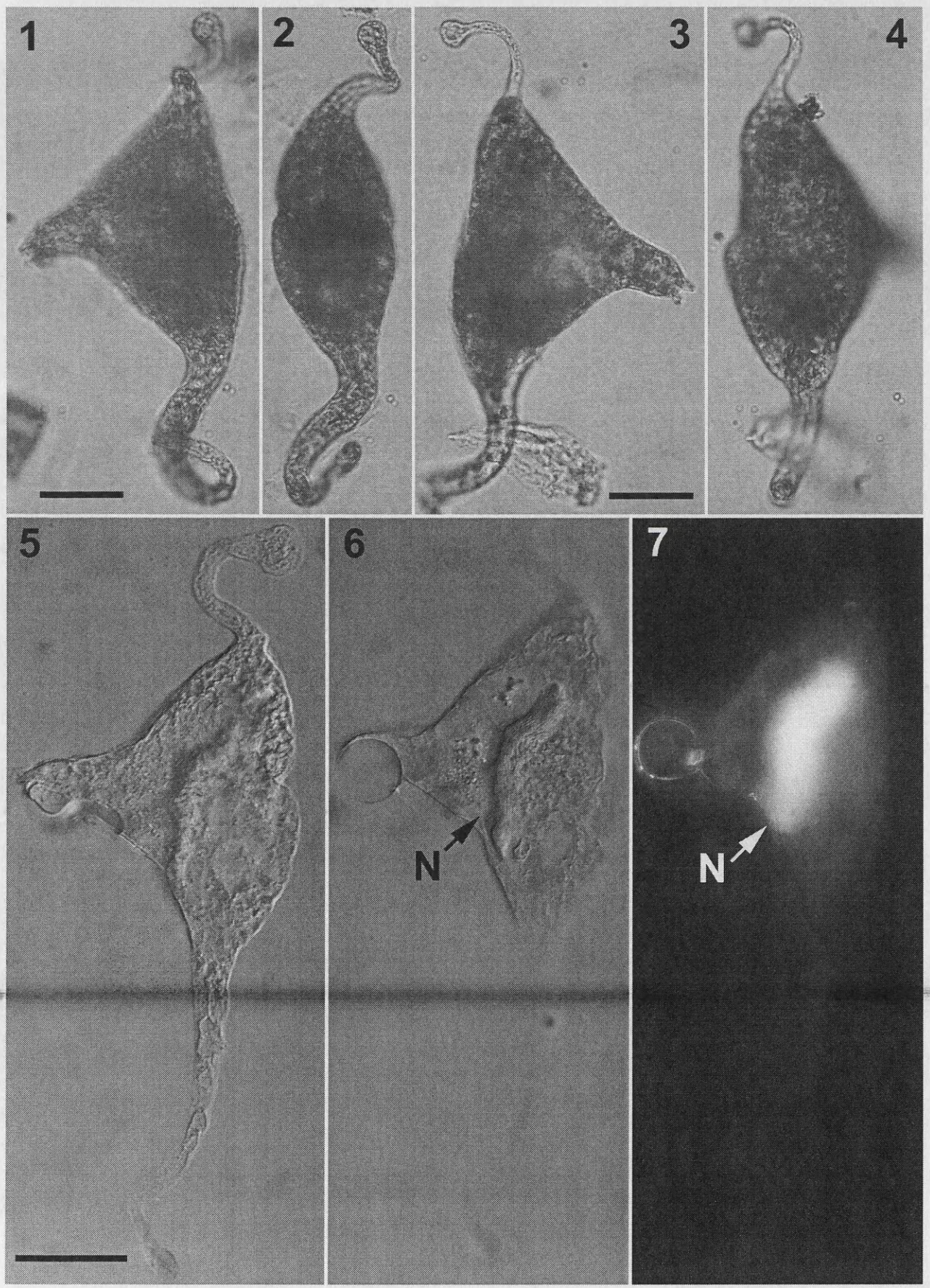
Station	Depth (m)	Latitude	Longitude	Date	W (μm)	L (μm)	Figures
6	-15	0°	160°E	15 Jan 2003	48	110	1-2, 8-13
6	-30	0°	160°E	15 Jan 2003	45	95	5-7
7	-30	0°	165°E	17 Jan 2003	52	105	-
8	-110	0°	170°E	18 Jan 2003	43	90	-
9	-15	0°	175°E	20 Jan 2003	55	110	-
9	-40	0°	175°E	20 Jan 2003	53	110	3-4
10	-40	0°	180°	21 Jan 2003	50	105	-

FIGURE LEGENDS

Figs. 1-7. Photomicrographs of *Gynogonadinium aequatoriale*, bright field optics. 1-2. Right lateral and ventral view of one specimen (also Figs. 8-13). 3-4. Another specimen in left lateral and ventral view. 5-6. Nomarski differential interference contrast (DIC) micrographs of another specimen. See nucleus in Fig. 6. 7. Epifluorescence photomicrographs of the same specimen stained with DAPI (4,6-diamidino-2-phenylindole) showing the nucleus glowing brightly under UV excitation. N= nucleus. Scale bars: 20 μm.

Figs. 9-13. *Gynogonadinium aequatoriale*, scanning electron micrographs (also Figures 1-2). 9-10. Left lateral and ventro-left lateral view, respectively. 10-11. Detail of the apical extension. The arrows indicates the apical groove. 12. Detail of the cingulum-sulcus area. See the flagellar pores. 13. Detail of the cingulum in the dorsal part of the cell. AG= apical groove C= cingulum; CL= cingular list; LFP = longitudinal flagellum pore; S= sulcus; TFP = transverse flagellum pore. Figs. 9-10, Scale bars: 20 μm. Figs. 11-13, Scale bars: 5 μm.

Figs. 14-15. *Gynogonadinium aequatoriale*, line drawings. 14. Left lateral and 15. ventral view, respectively. Scale bars: 20 μm.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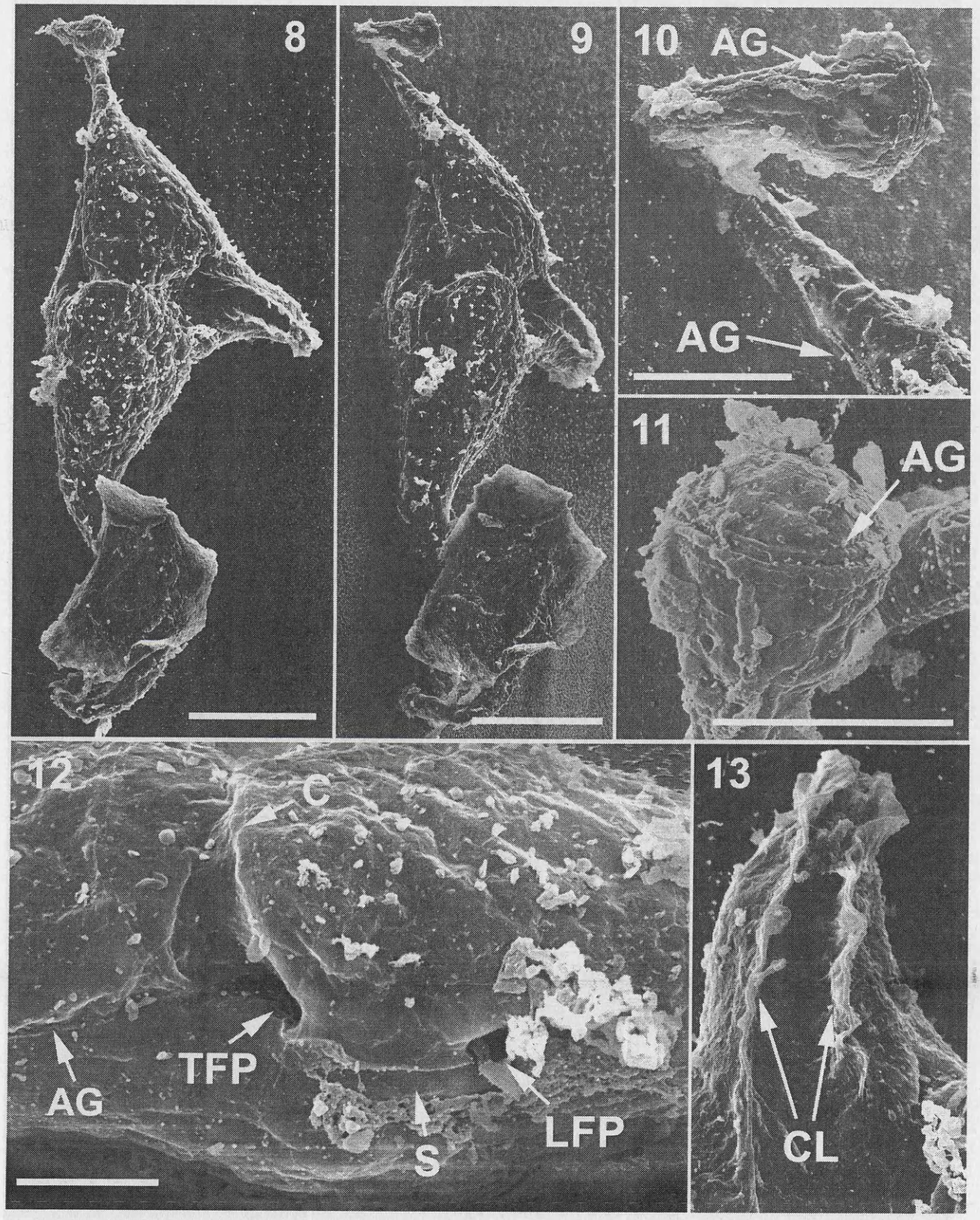
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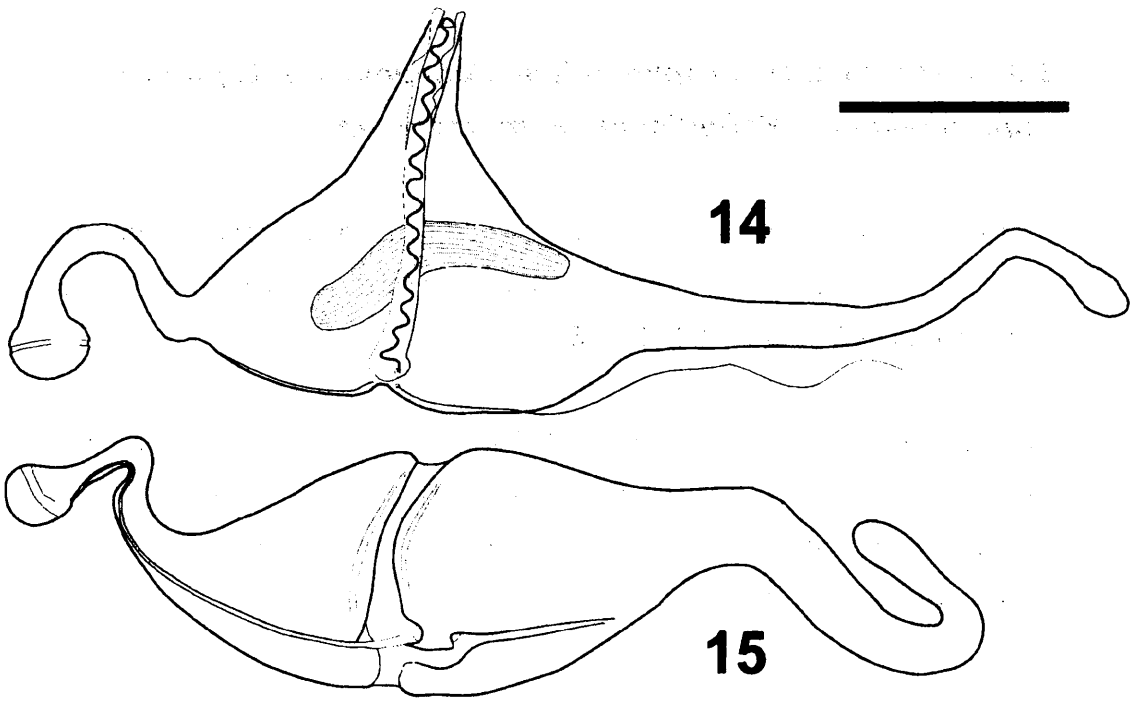
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15

3.2. Taxonomía y distribución de dinoflagelados poco conocidos:

3.2.4. Noctilucales: *Scaphodinium, Petalodinium, Leptodiscus, Spatulodinium, Kofoidinium, Pomatodinium.*

Gómez, F. & Furuya, K., 2004. New records of *Scaphodinium mirabile* (Dinophyceae), an unnoticed dinoflagellate in the Pacific Ocean. *Phycological Research* 52, 13-16.

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Phycological Research 2004; **52:** 13–16

Research note

New records of *Scaphodinium mirabile* (Dinophyceae), an unnoticed dinoflagellate in the Pacific Ocean

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SUMMARY

Previous records of dinoflagellate *Scaphodinium mirabile* Margalef (Leptodiscaceae, Noctilucales) were restricted to the Mediterranean-Black Sea and Eastern Atlantic Ocean. Nine and 34 specimens were observed in the upper 100 m layer in May and July, respectively, in a cross-section in the vicinity of the Kuroshio Current (NW Pacific Ocean). Nearly all the Lugol-fixed specimens appeared folded over themselves, an appearance that differs from the view reported in the scarce literature available.

Key words: aberrant dinoflagellate, Dinophyceae, Dinophyta, Kuroshio Current, Noctilucales, Pacific Ocean, phytoplankton, *Scaphodinium*, taxonomy.

The role of heterotrophic and mixotrophic phytoplankton, in particular dinoflagellates, on pelagic food webs has recently received significant attention (Gaines and Elbrächter 1987; Hansen 1991). However, among heterotrophic dinoflagellates, taxa belonging to the order Noctilucales Haeckel (see Gómez 2003 for a species list) have received less attention, with the exception of the red tide species *Noctiluca scintillans* (Macartney) Kofoid.

The morphology of the Noctilucales differs markedly from the Peridiniales, notably by the presence of contractile muscle-like fibrils involved in movements and cell shape changes (Cachon and Cachon-Enjumet 1964, 1966; Cachon and Cachon 1967a,b, 1969). Members of the family Leptodiscaceae F.J.R. Taylor are strongly flattened antero-posteriorly and display a wing-like extension (the velum) not associated with either the cingulum or the sulcus (Taylor 1976; p. 184; Fensome *et al.* 1993; p. 182; regarding the authorship of the family Leptodiscaceae see Fensome *et al.* 1993; p. 183).

Scaphodinium is an extremely flattened biflagellate cell, usually folded over one of its faces. The flattened portion is projected in both ends, with the extension closest to the nucleus being bilobulate, shorter and wider than the other. No sulcus or cingulum have been reported; the proximal parts of both flagella are sheathed in tube-like channels located next to the large, egg-shaped, encapsulated nucleus. No chloroplasts are present and the cytoplasm contains a uniform network of myo-fibrils (Cachon and Cachon 1969; Sournia 1986).

The type species of this monotypic genus, *Scaphodinium mirabile* Margalef, was originally described from the Spanish Mediterranean coastal waters (Margalef 1963). From the NW Mediterranean Sea, Cachon and Cachon-Enjumet (1964) reported the taxonomic junior synonym *Leptospathium navicula*. The species has been further reported in the Mediterranean Sea (Margalef 1969a,b; Léger 1971; Abboud-Abi Saab 1989; Gómez and Gorsky 2003), the Eastern Atlantic Ocean Margalef (1973, 1975) and recently from the Marmara and Black Seas (Balkis 2000; Stoyanova 1999).

This study reports for the first time *Scaphodinium mirabile* in the Pacific Ocean. Notes on the distribution, morphology, and on the reasons for the apparent underestimation of this species are given below.

The material was collected from two cruises (13–20 May and 3–10 July, 2002) aboard R/V *Soyo-maru* carried out along the meridian 138° in the vicinity of the Kuroshio Current. During the cruise in May, nine stations were sampled from 30°30′N to 34°15′N. In July 10 stations were sampled from 30°0′N to 34°20′N. At each station, 15 discrete depths from 5–200 m were sampled with Niskin bottles (Table 1). Seawater samples were preserved with acidified Lugol's solution (Hasle and Syvertsen 1997; p. 334) and stored at about 5°C. Samples were preconcentrated via settling in glass cylinders, and concentrates settled in standard sedimentation chambers. Concentrates equivalent to 400 mL were observed with a Nikon inverted microscope equipped with a Nikon digital camera. One specimen in the volume examined (1 cell/0.4 L) corresponds to 2.5 cells L^{-1}.

The number of samples analyzed was 131 in May and 144 in July, representing a total volume of 106 L of seawater examined in both cruises. In May nine specimens of *Scaphodinium* were found in eight samples (6% of the total samples), whereas in July, 34 specimens

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Table 1. Number of specimens of *Scaphodinium mirabile* collected at each sample (0.4 L) along the meridian 138°E

Station						May							July								
Latitude	C01 34°20′	B01 33°0′	C03 33°30′	C06 33°0′	C09 32°30′	C10 32°0′	C11 31°30′	C12 31°0′	C13 30°30′	B03 34°15′	B02 33°45′	C08 33°30′	C07 33°0′	C06 32°30′	C05 32°0′	C04 31°30′	C03 31°0′	C02 30°30′	B01 30°0′
Depth: -5	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0
-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
-20	0	I	0	1	I	0	0	0	I	1	1	0	0	3	0	1	0	0	0
-30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I	0	0	0	I
-40	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
-50	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
-60	0	0	0	0	0	0	0	0	0	0	2	2	1	0	0	0	2	0	0
-70	0	2	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1
-80	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0
-90	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
-100	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
-125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
-150	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	I
-175	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	I	I	0	I
-200	0	0	0	0	0	0	0	0	I	0	0	0	0	0	0	0	0	0	0

were found in 29 samples (20% of the total samples). The maximum number of specimens found in a single sample (0.4 L) was three (Table 1). Nearly all the specimens were recorded in the upper 100 m layer. The number of records was higher in the summer than in the spring (Table 1).

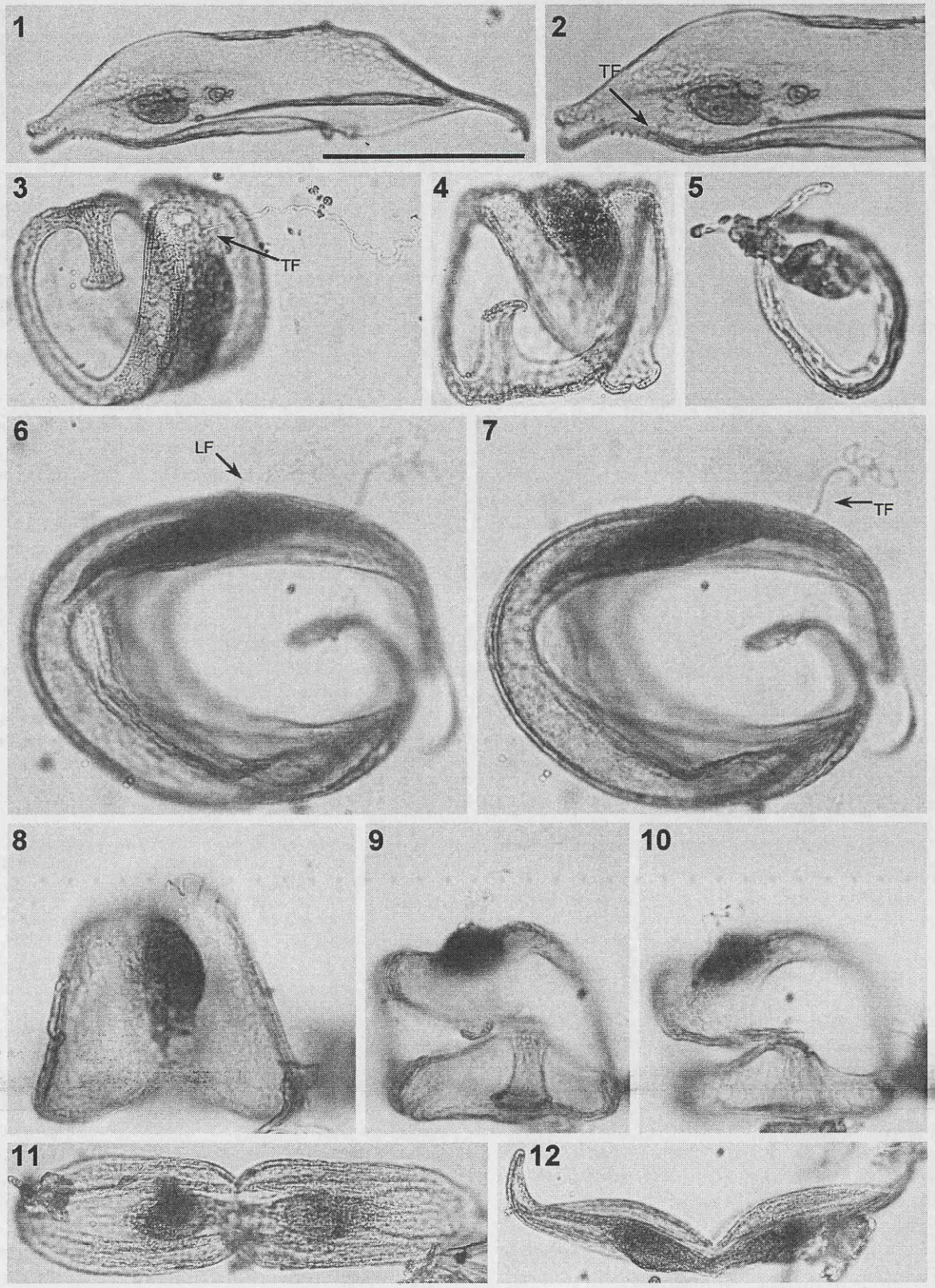
The morphology of leptodiscaceans results in a difficult interpretation of cell orientation. According to the interpretation by Cachon and Cachon (1969) the part of the cell containing the flagella is considered the hyposoma. During routine microscopical observation, the specimens appeared in several views with different appearances (Figs 1–4,6–12). The non-folded view found in the literature (Sournia 1986; fig. 143) was only found in two of 43 specimens observed (Figs 1,2). The flagella were not visible in most specimens, probably because they were lost as a result of the fixation. The transverse flagellum (TF), as defined by Cachon and Cachon (1969), is usually coil-shaped and larger than the longitudinal flagellum (Figs 2,3,8–10). The insertion of the TF is located between the nucleus and the bi-lobuled extremity (Figs 3,7). Fensome *et al.* (1993; p. 182) apparently followed the interpretation of the orientation by Cachon and Cachon (1969). However the orientation of the cell and the labeling of the flagella by Fensome *et al.* (1993; their fig. 186D) is the reverse of Cachon and Cachon (1969) interpretation and even the path of each flagellum is different.

Nearly all the Lugol-fixed specimens appeared folded, extremity against extremity (Figs 3,4,6–10). In lateral views, considered here as the view showing the extreme low thickness in relation to the cell body, the flagella appeared to the exterior side (Figs 3,6–10). One of the specimens observed was undergoing binary fission (Figs 11,12).

Scaphodinium can be considered homogeneously distributed in the euphotic zone, with no clear latitudinal trends, despite the studied area covering a wide range of hydrographical and trophic conditions. It can only be inferred that this taxon tends to be more abundant in the summer (Table 1). In the Black Sea, this species was also more common during the summer (Stoyanova 1999). The salinity does not seem to influence on the distribution of *Scaphodinium*, if it is

species as een recor e , rom t e sa ine waters o the eastern Mediterranean basin (salinity of 38–39) to the brackish waters of the Black Sea with salinity values of 15–18 (Stoyanova 1999). Concerning the trophic conditions, the eutrophic Black Sea waters strongly differ from the oligotrophy that prevails in the adjacent waters of the Kuroshio Current.

Despite its relatively large size, which renders the organisms easily collectable by net or bottle sampling, records of *Scaphodinium* are scarce. Other reasons for the underestimation of *Scaphodinium*, during routine analyses are:



Figs 1–12. Photomicrographs of *Scaphodinium mirabile* Margalef and (Fig. 5) of an appendicularian. 1,2. A non-folded specimen with a coil-shape transverse flagellum (TF). Scale bar = 100 μm (May St. 9, 80 m depth). 3,4. Two views of the same specimen. The arrow points at the insertion of the TF (July B02, 60 m depth). 5. An appendicularian here presented for a comparison to the lateral views of *Scaphodinium*. 6,7. Lateral views of a specimen showing the longitudinal (LF) and transverse flagella (July St. 3, 40 m depth). 8–10. Several views of the same specimen showing the TF (May St. 6, 20 m depth). 11,12. Two views of a specimen under division (July St. 6, 5 m depth).

1 *Scaphodinium* is usually missing in the literature used for phytoplankton identification, with the exception of Sournia (1986) and Fensome *et al.* (1993). The original description of the species (Margalef 1963) and further records (Cachon and Cachon-Enjumet 1964; Margalef 1969a,b, 1973, 1975; Léger 1971; Abboud-Abi Saab 1989; Stoyanova 1999; Balkis 2000) appeared in journals that are not easily accessible.
2 The morphology of leptodiscaceans is highly modified compared to typical dinoflagellates (Peridiniales). The lack of a cingulum, sulcus and the possible loss of the flagella by fixation, contribute to the difficulties in identification. In the microscope, Lugol-fixed cells of *Scaphodinium* appear in views with different appearances that only with difficulty can be considered as a dinoflagellate (Figs 1–4,6–10).
3 The photomicrographs or drawings reported in the literature show views of non-folded cells. However, in this study nearly all Lugol-fixed specimens were folded with no visible flagella, and may look like the damaged tail of an appendicularian to a non-experienced observer (Fig. 5).

In conclusion, correct identification of species of this group of heterotrophic dinoflagellates is a critical step in the evaluation of its role in pelagic food webs.

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Leptodiscaceans (Noctilucales, Dinophyceae) from the Pacific Ocean: First records of *Petalodinium* and *Leptodiscus* beyond the Mediterranean Sea

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Abstract

Records of dinoflagellates of the family Leptodiscaceae (Noctilucales) from the Kuroshio Current, Philippine, Celebes, Sulu, South China Seas and the western and central Equatorial Pacific Ocean are described. *Scaphodinium mirabile* was the most common leptodiscacean. Two specimens that differed from the type species of *Scaphodinium* were found: one specimen showed a highly bifurcate proximal extremity and another showed two dissimilar proboscides from the distal extremity. Another unidentified leptodiscacean showed an arrowhead-shaped contour with the margins folded. Six specimens of *Petalodinium porcelio* were found, being the first record beyond the Mediterranean-Black Seas. Six specimens were tentatively assigned to the genus *Leptodiscus*, being the first record beyond the western Mediterranean Sea. The folded specimens that ranged from 90 to 120 μm in diameter and with a prominent flagellum were tentatively considered to be young specimens of *Leptodiscus*. The abundance of the leptodiscaceans is underestimated in the world's oceans.

Keywords: *Scaphodinium*; *Petalodinium*; *Leptodiscus*; Noctilucales; Dinophyta; Pacific Ocean

Introduction

The Noctilucales Haeckel differ markedly from the rest of the dinoflagellates, notably by the presence of contractile muscle-like fibrils involved in cell shape changes and movements. The noctilucaceans have been placed as an order in the class Dinophyceae (Sournia 1986) or as the class Noctiluciphyceae Fensome et al. The family Leptodiscaceae Kofoid is the least known among the Noctilucales. Their cell bodies are strongly antero-posteriorly flattened with a bilateral symmetry or with equatorial wing-like expansions lacking the dome, being able to contract suddenly when the surrounding water is disturbed (Cachon and Cachon 1967, 1969, 1984, 1986). No chloroplasts have been reported. Neither sulcus nor cingulum has been reported. The leptodiscaceans comprise the monotypic genera *Cachonodinium* Loeblich III (= *Leptodinium* J. Cachon et M. Cachon), *Craspedotella* Kofoid, *Leptodiscus* Hertwig (= ?*Pratjetella* Lohmann), *Leptophyllus* J. Cachon et Cachon-Enjumet (= *Abedinium* Loeblich Jr et Loeblich

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III), *Petalodinium* J. Cachon et M. Cachon and *Scaphodinium* Margalef (= *Leptospathium* J. Cachon et Cachon-Enjumet). Cachon and Cachon-Enjumet (1964) and Cachon and Cachon (1967, 1969, 1984, 1986) carried out most of the studies on these taxa from the coastal waters of the Ligurian Sea (NW Mediterranean Sea). Since their observations, the records of leptodiscaceans have been scarce and several genera have never been reported after the initial descriptions.

The deformation due to preservation and the bizarre appearance of the leptodiscaceans compared to other dinoflagellates makes the detection of these species difficult. The leptodiscaceans are extremely delicate and easily deteriorate during sample treatment. The study of live specimens of dinoflagellates during oceanic research cruises is difficult and examples are scarce (Elbrächter 1979). Unfortunately the analysis of fixed samples is not comparable to the detailed studies on the morphology and the life cycle carried out by Cachon and Cachon (1967) and Cachon and Cachon (1969) from thousands of live specimens collected from coastal waters.

Little is known about the occurrence of the leptodiscaceans in oceanic waters. Recently Gómez and Furuya (2004) reported the presence of *Scaphodinium mirabile* in the Pacific Ocean for the first time from two cruises in the vicinity of the Kuroshio Current. This study deals with the leptodiscaceans recorded in further cruises in the western Pacific Ocean.

Material and methods

Samples were collected in the western Pacific Ocean: (1) Two cruises on board R/V *Soyo Maru* (13–20 May and 3–10 July 2002) along the 138°E meridian in the vicinity of the Kuroshio and adjacent waters. Nine stations were sampled from 30°30′N to 34°15′N in May, and 10 stations were sampled from 30°0′N to 34°20′N during the July cruise. At each station, 15 depths between 5 and 200 m were sampled; (2) cruise on board R/V *Hakuho Maru* (7 November–18 December 2002) to the Celebes, Sulu and South China Seas. Samples were collected from 10 stations at six depths between the surface to 150 m depth; (3) on board R/V *Mirai* (15–28 January 2003) along the equator from 160°E to 160°W. Samples were collected from nine stations at 14 depths between 0 and 200 m depth; (4) Six cruises were carried out at Stn. H on board R/V *Oshoro Maru* and Stn. A7 on board R/V *Wakataka Maru* in the Oyashio area during the spring and summer of 2003; (5) In addition, nine samples were collected from 5 to 100 m depth in a coastal station off Oshima Island, Sagami Bay (34°39.2′N, 139°31.3′E) on 7 June 2003 (Fig. 1).

All samples were collected with Niskin bottles, preserved with acidified Lugol's solution and stored at 5 °C. Sub-samples (400 mL) were allowed to settle in glass sedimentation cylinders. The top 350 mL of each sample was siphoned off progressively over 5 days using a length of small-bore tubing. The remaining 50 mL was settled in composite sedimentation chambers and observed using a Nikon inverted microscope.

Several of the Lugol-fixed specimens were isolated from the chambers with a capillary, transferred to a glass slide, and observed with an Olympus microscope equipped with Nomarski Differential Interference Contrast (DIC) system and photographed at × 600 or × 1000. To show the location of the nucleus one of the specimens was stained with DAPI (4,6-dianidino-2-

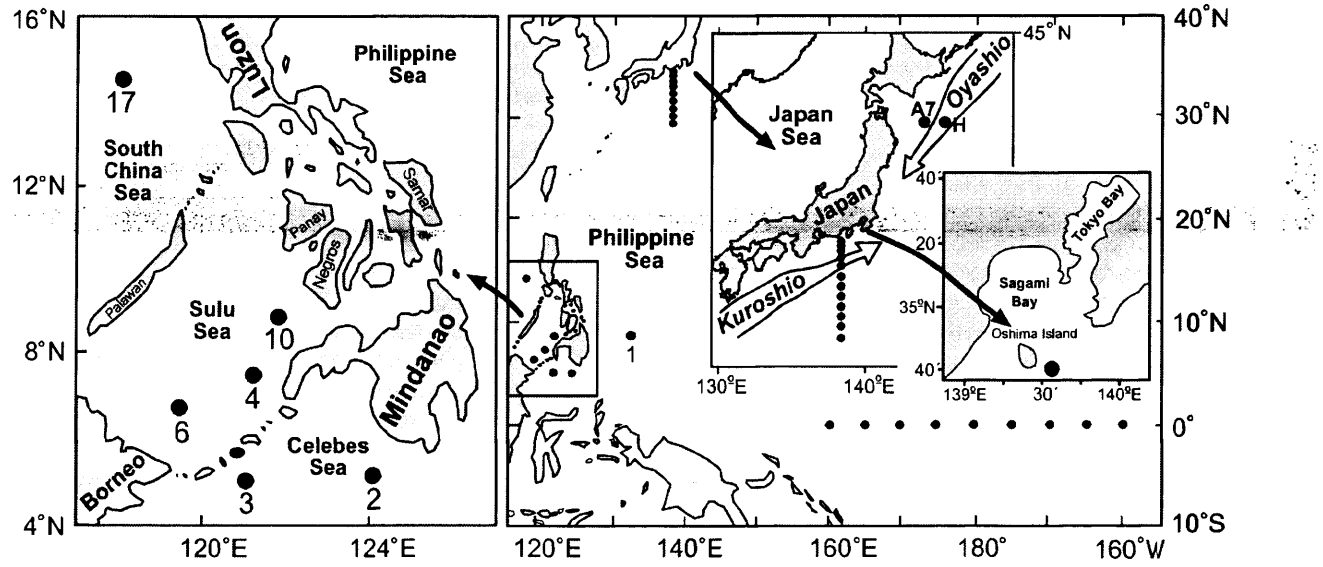


Fig. 1. Map of the station locations in the western Pacific Ocean. The insets show the Kuroshio Current and the Sagami Bay in the south Japan, and the Celebes, Sulu and South China Seas.

phenylindole) and examined with an Olympus epifluorescence microscope.

Results and discussion

Scaphodinium Margalef

Scaphodinium is an extremely flattened cell that contains a uniform network of myo-fibrils. The flattened portion projects at both ends, with the extremity closer to the nucleus (here considered as the proximal part) bilobulate, shorter and wider than the other spatula-shaped extremity (here considered as the distal part). Two flagella were located next to the large, egg-shaped, encapsulated nucleus. According to the orientation proposed by Cachon and Cachon (1969) the transverse flagellum was undulate, larger and sheathed in a tube-like channel in the proximal part; the longitudinal flagellum was shorter and rarely observed from fixed specimens. Nearly every one of the Lugol-fixed specimens appeared folded over one of its faces with the flagella on the convex surface (Gómez and Furuya 2004).

In the vicinity of the Kuroshio Current 9 and 34 specimens of *S. mirabile* were found in May and July, respectively (Gómez and Furuya 2004). In the marginal seas of the western Pacific Ocean seven specimens were found, mainly in the more productive waters of the Celebes Sea. In the equatorial Pacific Ocean, only six specimens were found, nearly all in the frontal zone between the western Pacific warm pool and the Equatorial Upwelling Regimen (Table 1, Fig. 2). In the coastal waters of Sagami Bay, off Oshima Island, three specimens were collected. No leptodiscaceans were observed in the subarctic waters of the Oyashio Current.

Nearly all the specimens corresponded to *S. mirabile*, characterized by a slightly bifurcate proximal extremity and the spatula-shaped distal extremity. Two specimens that did not agree with the general characteristics of the type species were observed: One specimen, *Scaphodinium* sp1, showed a high degree of bifurcation of the proximal extremity (Figs. 3–5, Table 1). The distal extremity was lobulate, lacking the spatula-shaped contour of the type species (Fig. 4). Another specimen, *Scaphodinium* sp2, showed larger differences compared to the type species (Figs. 6–11). From the distal extremity arose two different proboscides: a small rounded proboscis and a large acute proboscis of about 1/4 of the cell length (Figs. 6 and 7). The proximal extremity was slightly bifurcated (Fig. 8). Assuming a bilateral symmetry, the nucleus was slightly marginally located (Figs. 9 and 10). A step-like discontinuity was observed in the margin of the specimen more distal from the nucleus (Fig. 11).

A specimen of comparable shape, that cannot be ascribed to any of the known genera of leptodiscaceans, was also found. The outline of this cell was arrowhead-shaped and the proximal extremity bifurcated. The margins of the cell appeared folded as far as the region of the nucleus (Figs. 12 and 13, Table 1).

Petalodinium Cachon et Cachon

Petalodinium is an also an extremely flattened taxon. The proximal extremity is slightly more acute than the

Table 1. Records of leptodicaceans (excluding *Scaphodinium mirabile*) in the western Pacific Ocean

Taxon	Date	Depth	Latitude	Longitude	Length	Figure
Scaphodinium sp1 (highly bifurcated)	9/05/2002	70	33°N	138°E	170	Figs. 3–5
Scaphodinium sp2 (with proboscides)	10/05/2002	150	33°30′N	138°E	150	Figs. 6–11
Arrowhead-shaped leptodiscacean	11/12/2002	100	14°30′N	118°E	120	Figs. 12 and 13
Petalodinium porcelio	4/07/2002	40	30°N	138°E	[a]	Figs. 14 and 15
Petalodinium porcelio	11/12/2002	75	14°30′N	118°E	380	Figs. 16 and 17
Petalodinium porcelio	8/07/2002	40	33°45′N	138°E	370	Fig. 18
Petalodinium porcelio	17/11/2002	30	5°N	121°E	360	—
Petalodinium porcelio	18/11/2002	50	5°N	121°E	350	Figs. 19–21
Petalodinium porcelio	15/01/2003	110	0°	160°E	[a]	—
Leptodiscus sp.	19/11/2002	75	7°25.3′N	121°12.5′E	110	Figs. 22–24
Leptodiscus sp.	17/01/2003	0	0°	165°E	120	Figs. 25–28
Leptodiscus sp.	07/06/2003	50	34°39.2′N	139°31.3′E	100	Figs. 29 and 30
Leptodiscus sp.	06/07/2002	70	32°N	138°E	90	Fig. 31
Leptodiscus sp.	04/07/2002	40	30°N	138°E	115	Fig. 32
Leptodiscus sp.	07/07/2002	70	34°15′N	138°E	110	Fig. 33

Date; depth (in meters); geographic coordinates (latitude, longitude); and total length (units as micrometers) of each record (diameter of folded specimens of *Leptodiscus*).

[a] Folded specimens of *Petalodinium porcelio*.

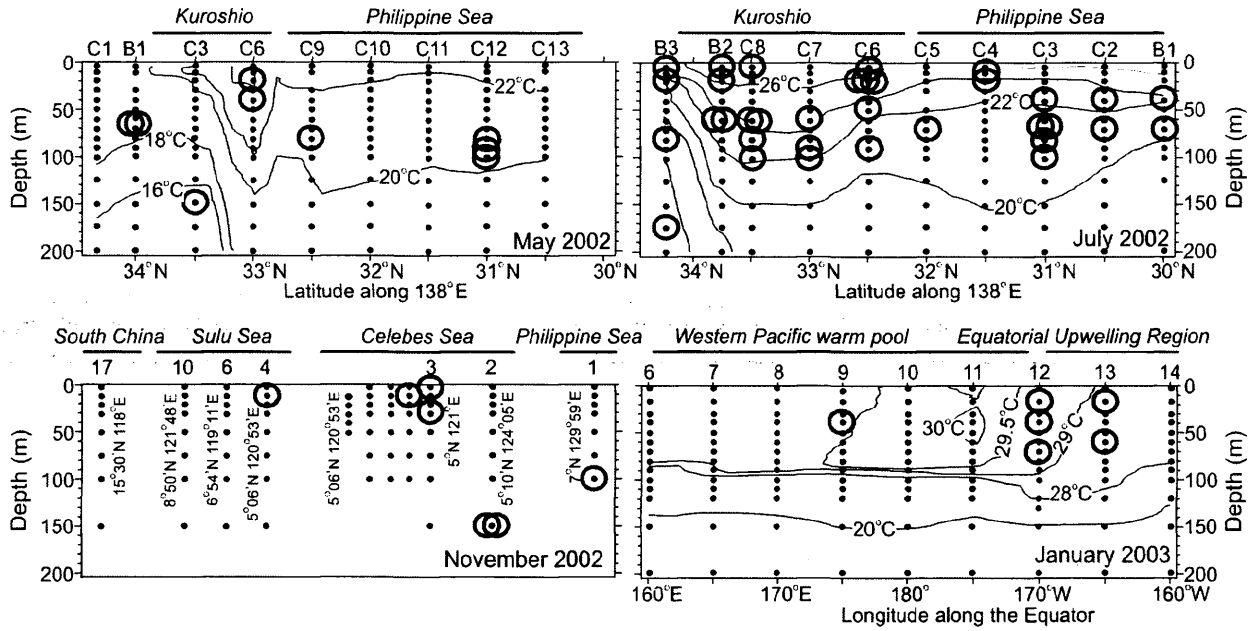


Fig. 2. Section plot of the records (marked by circles) of *Scaphodinium mirabile* in the western Pacific Ocean. Isotherms are shown.

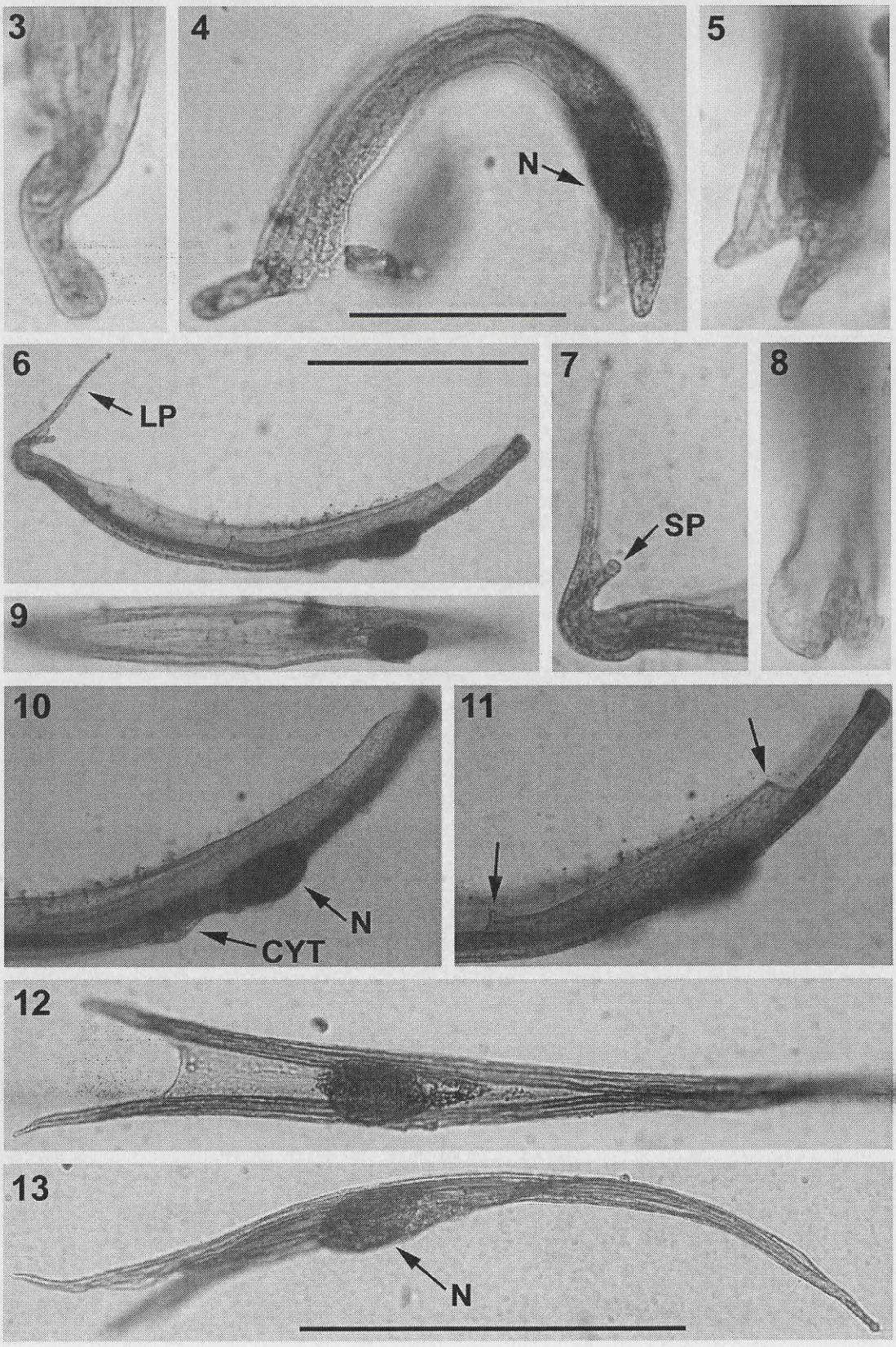
distal one. As in *Scaphodinium*, the transverse flagellum is partially in a tube-like channel close to a big egg-shaped, encapsulate nucleus. The longitudinal flagellum is shorter and it is difficult to observe from the fixed material. The most distinctive characteristic is the network of myo-fibrils with rectangular contours that uniformly covers the cell (Cachon and Cachon 1969; Sournia 1986). The type species was described from surface hauls from the Ligurian Sea (Cachon and Cachon 1969) with no further records in the Mediterranean Sea. Later Stoyanova (1999) reported a high abundance of *Petalodinium porcelio* in the coastal waters of the western Black Sea, also with no further records.

During the present study six specimens of *Petalodinium* were found (Table 1). Two of the specimens appeared folded over themselves with an appearance that closely resembled *S. mirabile* (Figs. 14 and 15). However, the network of fibrils with prominent rectangular contour differed from the less marked and more irregular reticulation of *Scaphodinium*. Another specimen had a more elongate appearance and the margins partially folded (Figs. 16 and 17). The reticulation of the specimens was visible under bright field optics (Fig. 18) and even clearer under DIC optics (Fig. 19). The transverse flagellum was partially sheathed in a tube-like channel (Fig. 20). After DAPI-staining the nucleus glowed brightly under UV excitation (Fig. 21). The nucleus was large as in *Noctiluca scintillans* (Macartney) Kofoid, which ultrastructure has been investigated (Soyer 1969, 1972). Assuming the similarity with *Noctiluca*, the nucleoli could occupy 1/3 of the nuclear mass and the black round spots in the surface of the nucleus and its periphery were considered as the nuclear ampullae (Soyer 1969) (Figs. 20 and 21).

Leptodiscus medusoides Hertwig

The type genus of the family Leptodiscaceae has the form of a medusa with a contractile margin. A single flagellum arose from a blind tube on the convex surface. The nucleus and the cytostome were centrally located on the top of the cell (Cachon and Cachon 1969). According to Cachon (1964) the parasitic dinoflagellate

Figs. 3–13. Photomicrographs of leptodiscaceans, bright field optics. **3–5,** *Scaphodinium* sp1 (highly bifurcated). **3,** Detail of the distal extremity. **5,** Details of the bifurcate proximal extremity. **6–11,** *Scaphodinium* sp2 (with proboscides). **6,** See the short and the large acute proboscides in the distal extremity. **7,** Details of the short proboscis. **8,** Details of the bifurcate proximal extremity. **9,** See the nucleus marginally located. **10,** See the nucleus and the cytostome region. **11,** Details of the step-like discontinuity in the cell margin more distal from the nucleus. **12–13,** Arrowhead-shaped leptodiscacean with the margins folded. See Table 1 for the location of the records. N = nucleus; CYT = cytostome; LP = large proboscis; SP = short proboscis. Scale bars: 50 μm.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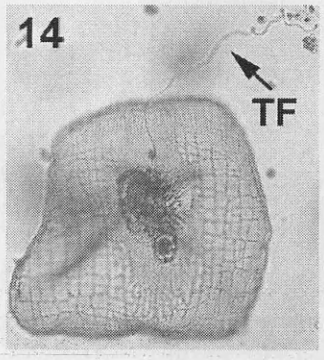
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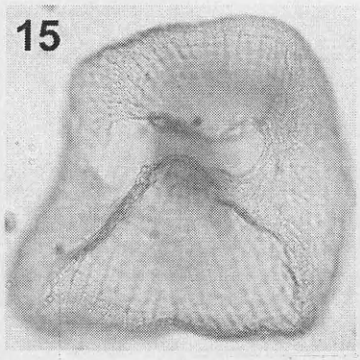
TF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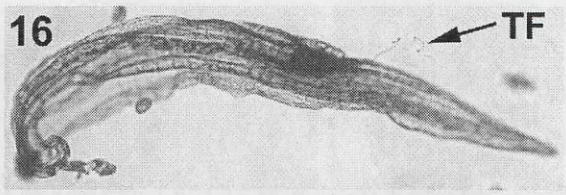
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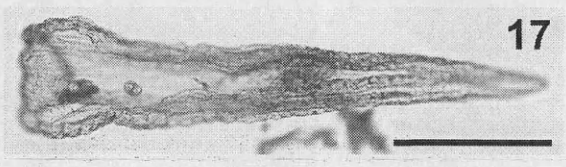
TF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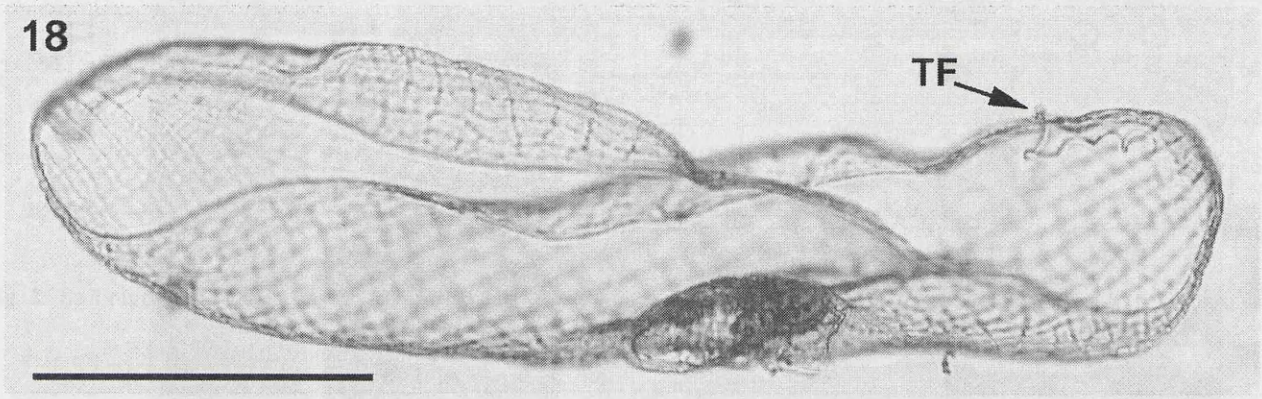
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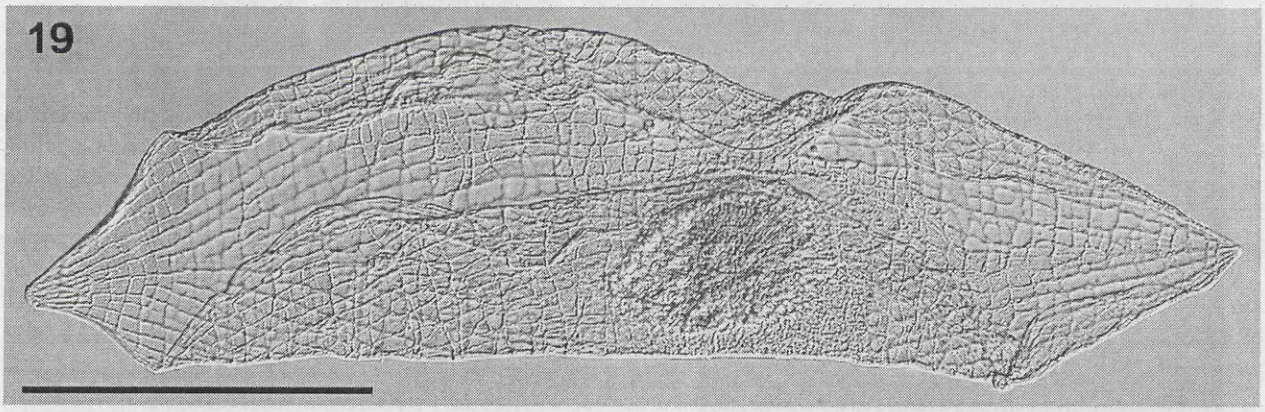
TF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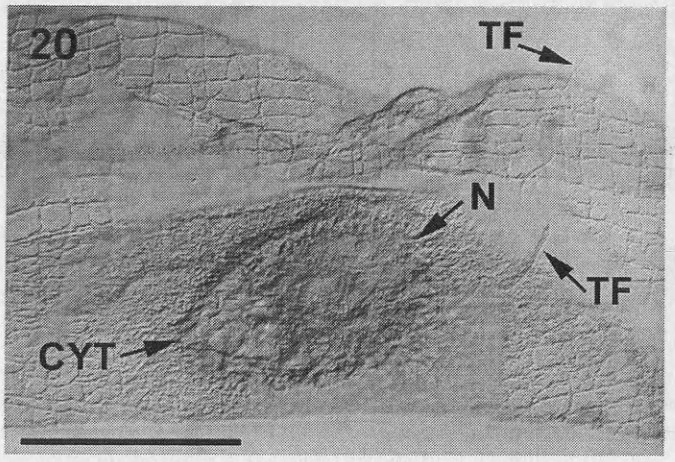
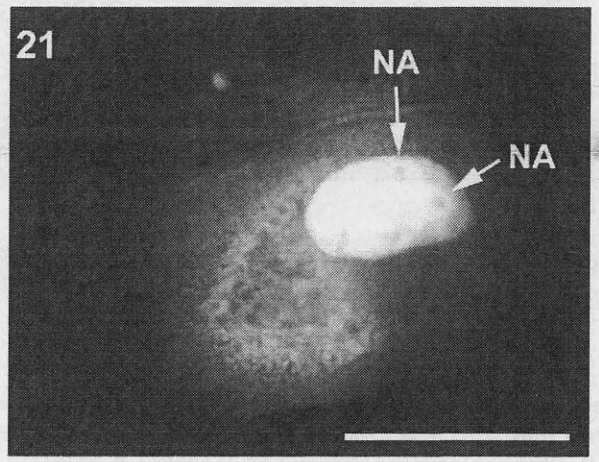

20
TF
N
TF
CYT


21
NA
NA

Amoebophrya leptodisci Cachon infests the region of the nucleus. The circular contour of *Leptodiscus* and the lack of a prominent reticulation prevent this taxon being confused with folded specimens of other leptodicaceans such as *Petalodinium*.

Hertwig (1877) described *L. medusoides* from the port of Messina (Sicily), being further exclusively reported in other areas of the western Mediterranean Sea (Cachon and Cachon 1969; Margalef 1969; Vila et al. 2001). According to Cachon and Cachon (1969) this taxon was common in surface waters under calm conditions. These authors remarked that *Leptodiscus* was very easily destroyed during sample collection. Despite the probable underestimation of its abundance, Cachon and Cachon (1969) reported abundances of 80 cells L^{-1}. Taking into account that this taxon can reach 2 mm in diameter, this constitutes a high biomass. Vila et al. (2001) considered *L. medusoides* as a potentially harmful species because it was associated with dense mucilage able to cause the breakage of fishermen's nets. Until now the distribution of *Leptodiscus* seems to be restricted to the western Mediterranean Sea. If the doubtful genus *Pratjetella* is accepted as a synonym (see discussion in Sournia, 1986, p. 112), *Leptodiscus* could also occur in the Atlantic Ocean.

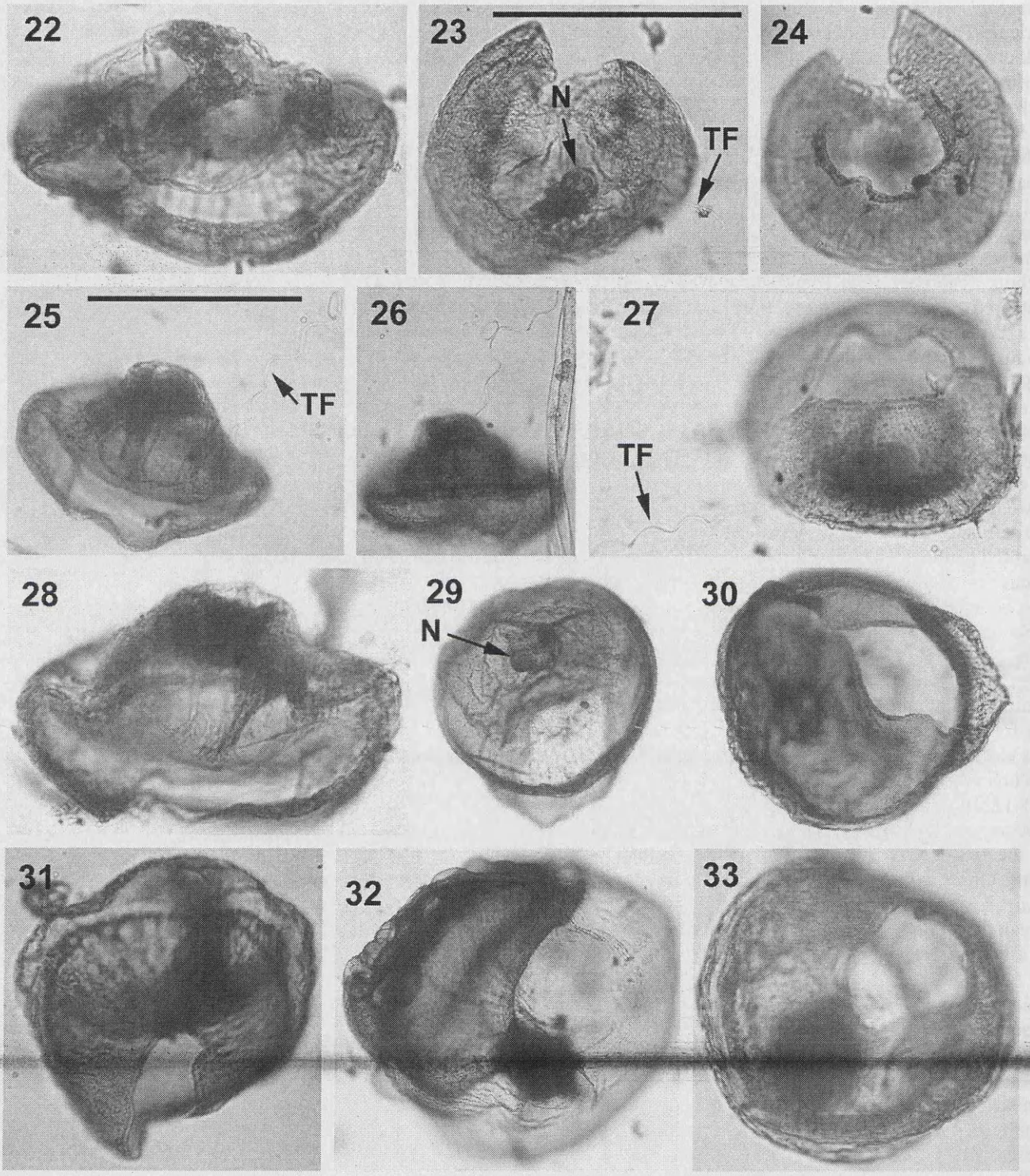
Six-folded leptodiscaceans with a medusoid shape were tentatively assigned to the genus *Leptodiscus* (Figs. 22–33, Table 1). Several specimens, after sample treatment, maintained a well-developed flagellum arising from the convex side. The length of the flagellum was close to the diameter of the folded cell (~100 μm). According to Hertwig (1877) the cell diameter was 600–1500 μm and Cachon and Cachon (1969) found specimens of 2000 μm. In the present study, the diameter of the specimens observed was smaller than 120 μm, being closer to the other medusoid leptodiscacean, *Craspedotella pileous*, described from the tropical Pacific Ocean (Kofoid 1905). The shape of *Craspedotella*, close to a hydromedusa, is even more medusiform than that of *Leptodiscus*. Cachon and Cachon (1969) found *C. pileous* in very deep waters (>300 m depth), but their observations did not agree with Kofoid's original from the eastern Atlantic Ocean. No information is available on the occurrence of flagella in *Craspedotella*. Due to the occurrence of flagella, the specimens of the present study were not assigned to *Craspedotella*. The well-developed flagellum, considered as the transverse flagellum following Cachon and Cachon (1969), was preserved in three of the six specimens observed. The percentage of individuals that maintained the flagellum after fixation in *Leptodiscus* was higher than for the Lugol-fixed cells of *S. mirabile*.

Even folded, the diameter of the individuals observed in the present study (90–120 μm) was not in accordance with the 600–2000 μm of diameter reported for *Leptodiscus* in the literature (Sournia 1986, p. 53). Cachon and Cachon (1969, p. 27) reported the occurrence of small individuals of *Leptodiscus* of about 100 μm in diameter. They suggested that these specimens result directly from sporogenetic reproduction, whereas the larger specimens (>700 μm) resulted from reproduction by bipartition. Cachon and Cachon-Enjumet (1964) only found six specimens in sporogenesis after examining 10,000 individuals. These authors also found differences in the chemical composition between the small and large forms. It cannot be disputed that this feature could favour the preservation of the smaller specimens. According to Cachon and Cachon (1969) the adults of *Leptodiscus* were extremely fragile and disintegrated very easily. No large specimens were observed in the present study. It can be hypothesised that the few small specimens observed during the present study constitute a fraction of a more numerous population of *Leptodiscus*.

According to Cachon and Cachon (1969, p. 25) the transverse flagellum is well developed, especially in the young trophonts. They reported that the transverse flagellum did not grow proportionally, keeping the same length in both young trophonts and adults of 2000 μm in diameter. They also reported that the flagellum provided efficient propulsion in the young specimens whereas in the large specimens it only produced a current towards the cytostome. The longitudinal flagellum of *Leptodiscus* (<5 μm long), which is not easily visible, is regarded as vestigial (Cachon and Cachon 1969, p. 25).

There may be considerable diversity of leptodiscaceans yet to be described. The fragility, transparency and polymorphism of the leptodiscaceans are responsible for the scarce records, going unnoticed in the leptodiscaceans are important for the evolution of the dinoflagellates, but molecular phylogenetical studies have not yet been applied. More work, including the development of appropriate fixation techniques for these organisms, is necessary.

Figs. 14–21. Photomicrographs of *Petalodinium porcelio*. **14–18,** Bright field optics. **14–15,** Two views of a folded specimen. **16–17,** Another specimen. See the flagellum. **18,** Non-folded specimen. **19–21,** Specimen observed under DIC and epifluorescence microscopy. **20,** See the flagellum partially encapsulated. **21,** The specimen stained with DAPI showing the nucleus glowing brightly under UV excitation. The arrows point the black round spots considered as nuclear ampullae. See Table 1 for the location of the records. CYT = cytostome; N = nucleus; NA = nuclear ampulla; TF = transverse flagellum. Scale bars, Figs. **14–19**: 100 μm and Figs. **20** and **21**: 50 μm.



Figs. 22–33. Photomicrographs of *Leptodiscus* sp., bright field optics. **22–24,** Damaged specimen with the transverse flagellum. **25–28,** Another specimen; see the prominent flagellum. **29–30,** Two views of a further specimen. **31–33,** Three different specimens. See Table 1 for location of the records. N = nucleus; TF = transverse flagellum. Scale bars: 100 μm.

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Kofoidinium, Spatulodinium and other kofoidiniaceans (Noctilucales, Dinophyceae) in the Pacific Ocean

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Abstract

Examples of rarely reported dinoflagellates of the family Kofoidiniaceae F.J.R. Taylor (Noctilucales) from the northwest, equatorial and southeast Pacific Ocean are described and illustrated. *Kofoidinium* was the most ubiquitous genus with a maximum abundance of 10 cells L^{-1}. Specimens of this genus were identified to four species: *Kofoidinium* sp. that showed a pointed extension that emerges from the antero-ventral region and *K. velelloides*, both of which had diameters that ranged from 40 to 200 μm; *Kofoidinium pavillardii* which showed a rounded epitheca and a larger size (~300–700 μm in diameter); and another species, tentatively identified as *K. splendens*, that contained red circular inclusions. Further research is needed to clarify the characteristics that separate *K. splendens* from the other species. This study is the first to record the genus *Spatulodinium* in tropical waters and in the southern hemisphere. *S* cf. *pseudonoctiluca* was found in the southeast Pacific Ocean, as well as other smaller specimens with a different shape or disposition of the tentacle that may belong to two other species. In the northwest and equatorial Pacific, specimens of *Spatulodinium* showed a green pigmentation that suggested the existence of the first species known in the order Noctilucales to contain its own chloroplasts. Immature stages of kofoidiniaceans, some containing symbiotic microalgae, are illustrated, as well as mature stages related to *Pomatodinium* and to unknown genera of kofoidiniaceans. Kofoidiniaceans are shown to be common and widely distributed in the Pacific, and are probably also frequent in other oceans, but are rarely recognised.

Keywords: *Kofoidinium*; *Spatulodinium*; *Pomatodinium*; Noctilucales; Dinophyta; Pacific Ocean

Introductio

The noctilucaceans, whose morphology differs strongly from that of typical Peridiniales, are of particular interest in the evolution of the dinoflagellates. After *Noctiluca scintillans* (Macartney) Kofoid, members of the family Kofoidiniaceae are the most common noctilucaceans. However information on this group has and Cachon (1967b). They demonstrated that the kofoidiniaceans undergo an exceptional morphological transformation during their life cycle, e.g., they described 6 stages, *a* to *f*, in *Kofoidinium pavillardii*, and they showed that several life stages had been described as separate species (Cachon and Cachon 1967b).

Pouchet (1885) described the first kofoidiniacean, *Gymnodinium pseudonoctiluca*. He already noted the strong morphological changes of this taxon and illustrated this single species with different morpholo-

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gies. One of the forms corresponded to a large *Amphidinium*-like cell, and the mature stage was a round or oval, laterally compressed cell with a tentacle. However, further authors considered the immature stages as separate species such as *Gymnodinium pyrocystis* Jørgensen, *G. fulgens* Kofoid et Swezy, *G. lebouriae* Pavillard and *G. viridis* Lebour (= *G. conicum* Kofoid et Swezy) (Cachon and Cachon 1967b; Konovalova and Selina 2002). Specimens from the NW Mediterranean Sea, illustrated by Pavillard (1921) under the name *Gymnodinium pseudonoctiluca*, were probably immature stages of *Kofoidinium*. Later, Pavillard found the mature stage, which he described as a member of a new genus and named it *Kofoidinium velelloides* (Pavillard, 1928). Another doubtful species, described from Canadian arctic waters, is *Kofoidinium arcticum*, known only from the first description (Bursa 1964). Cachon and Cachon (1967b) erected the genus *Spatulodinium* from *Gymnodinium pseudonoctiluca* and described the species *Kofoidinium pavillardii* Cachon et Cachon, 1967 and *K. splendens* Cachon et Cachon, 1967. They regarded *G. pseudonoctiluca* Pouchet, 1885 as the basionym for both *Spatulodinium* and *Kofoidinium* because the immature stages of these genera were similar in morphology.

Two other genera, *Pomatodinium* Cachon et Cachon-Enjumet, 1966 and *Cymbodinium* J. Cachon et M. Cachon, 1967, have been included in the family Kofoidiniaceae (Sournia 1986). *Pomatodinium* has the shape of a gastropod larva and may contain zooxanthellae (Cachon and Cachon-Enjumet 1966). The genus *Cymbodinium* has the shape of a veliger larva and only one flagellum has been observed (Cachon and Cachon 1967a). *Cymbodinium*, the least known of these genera, was first placed in the family Leptodiscaceae Kofoid and later in the family Kofoidiniaceae F.J.R. Taylor (Sournia 1986).

Information on the life cycle and detailed morphology of kofodinianceans is nearly restricted to the study based on live specimens collected by Cachon and Cachon in the coastal Ligurian Sea (NW Mediterranean). Little is known about the distribution and morphology of kofoidiniaceans in oceanic waters. However, they are probably often present in oceanic plankton samples, but are rarely recognised in the fixed condition. The present study investigates the distribution of kofoidiniaceans in several regions of the Pacific Ocean and illustrates the appearance of these dinoflagellates in fixed samples in the hope that they will be more commonly recognised and reported. The occurrence of body inclusions and tentative symbiotic microalgae is illustrated. Several life stages such as *Gymnodinium lebouriae* or *G. pseudonoctiluca* and other unidentified immature stages are illustrated. This study illustrates unknown species thought to belong to the genus *Spatulodinium* and other unknown genera of kofoidinaceans, including the first species in the order Noctilucales thought to contain its own chloroplasts.

Material and methods

Sample collection and light microscopical methods used in the northwest and Equatorial Pacific Ocean were described in Gómez and Furuya (2005) and are not repeated here. In the southeast Pacific Ocean, samples were collected during the BIOSOPE (Biogeochemistry and Optics South Pacific Experiment) cruise on board R/V *L'Atalante* from the Marquesas Is. to the coast of Chile (26 October-12 December 2004) (Fig. 1). Samples

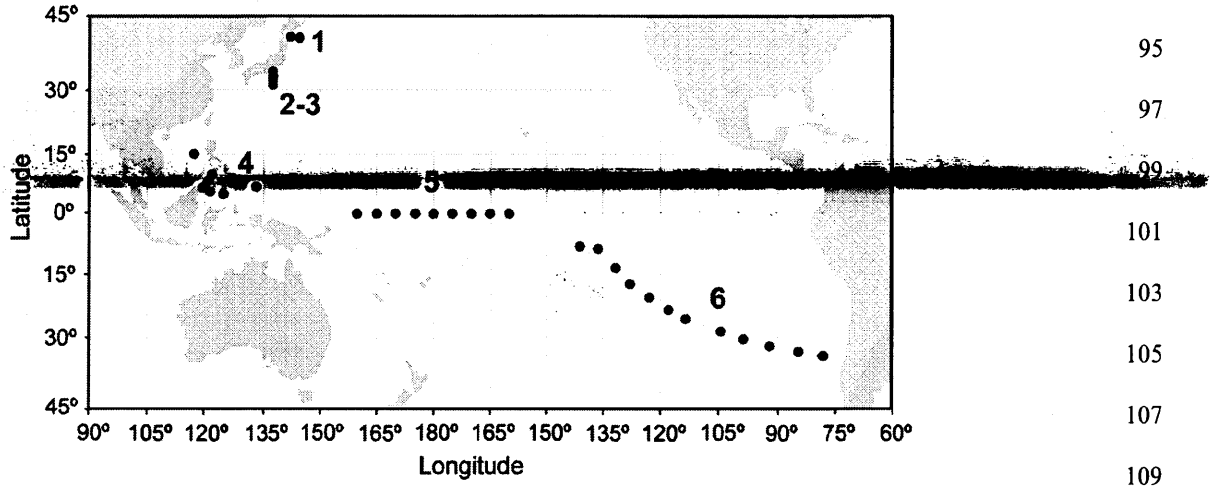

Fig. 1. Map of the station locations in the Pacific Ocean (marked by circles). 1. Oyashio Current. 2, 3. Kuroshio Current and Philippine Sea in May and July, respectively. 4. Celebes, Sulu and South China seas. 5. Western and central equatorial Pacific. 6. Southeast Pacific Ocean.

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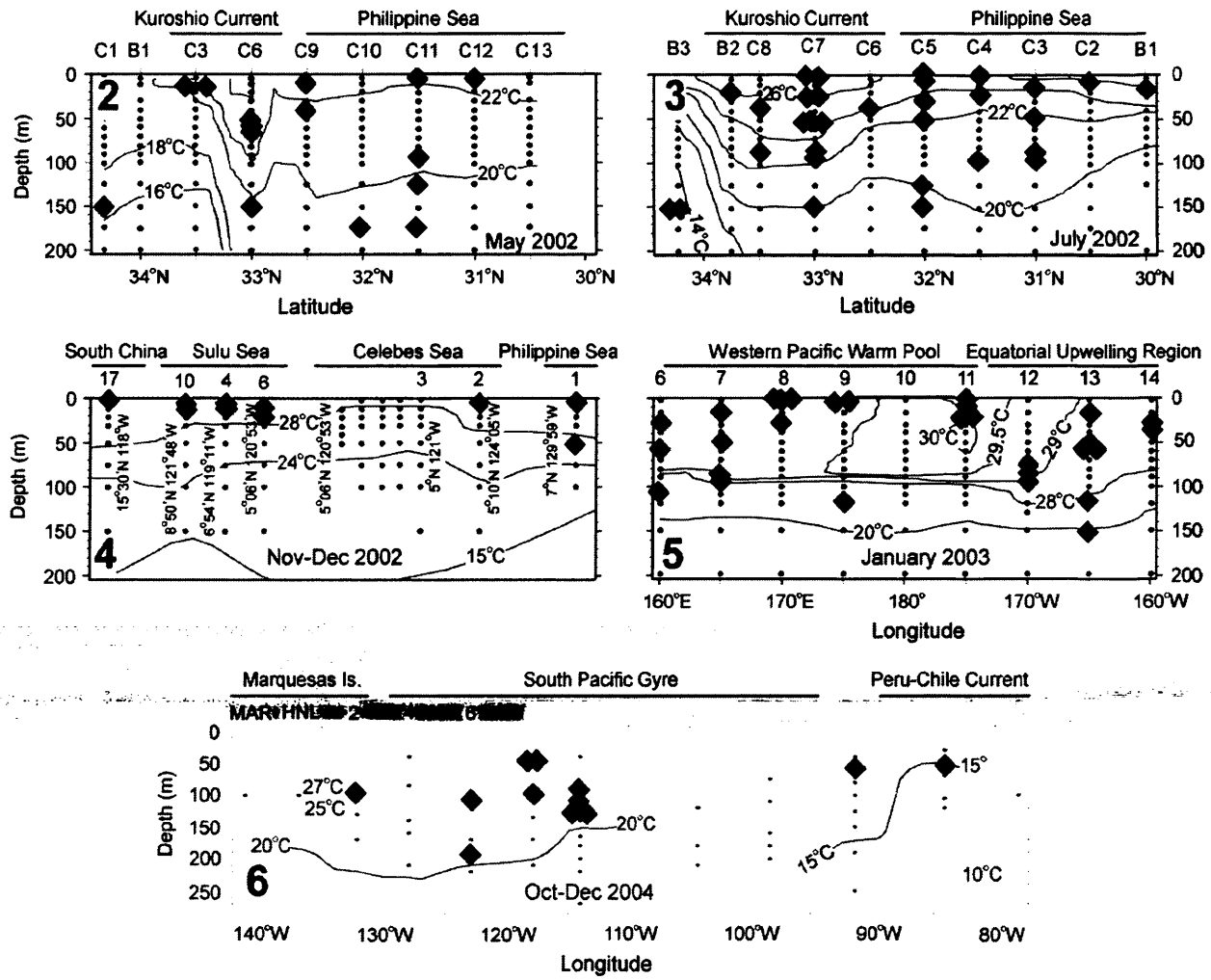
from 12 stations comprised 83 samples collected by Niskin bottles from 5 to 270 m depth. These were preserved with acidified Lugol's solution and stored at 5 °C. Samples of 500 mL were concentrated via sedimentation in glass cylinders. The top 450 mL of sample was slowly siphoned off with small-bore tubing during 6 days. The remaining 50 mL of concentrate, representing 500 mL whole water, was then settled in composite settling chambers. The entire chamber was scanned at 200× with an IX71 Olympus inverted microscope equipped with an Olympus digital camera. Each specimen was photographed and measured at 400× with Olympus DP70-BSW software.

Results

Distribution of *Kofoidinium*

Kofoidinium was the most ubiquitous genus of noctilucaceans in the open waters of the Pacific Ocean. A latitudinal transect in the vicinity of the Kuroshio Current to the south of Japan (138°E) was investigated in May and July 2002. In May, 15 individuals of *Kofoidinium* were found from 131 samples analysed (Fig. 2), and in July, 32 specimens were found in 144 samples analysed (Fig. 3). During the cruise in the marginal seas of the western Pacific Ocean 10 specimens were observed from 81 samples (Fig. 4). In the western and central equatorial Pacific 30 specimens were found from 124 samples (Fig. 5). In the southeast Pacific



Figs 2–6. Section plots of the records of *Kofoidinium* (mature stage) in the Pacific Ocean indicated by filled rhombuses (see also Fig. 1). **2**, Records along the meridian 138°E in May. **3**, Records from the same location in July. **4**, Records from Celebes, Sulu and South China seas. **5**, Records from the western and central equatorial Pacific. **6**, Records from the southeast Pacific. Isotherms are shown.

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Ocean, 42 specimens of *Kofoidinium* were found in the 83 samples analysed (Fig. 6). No kofoidiniaceans were found in the sub-arctic waters of the Oyashio Current off Hokkaido.

It is difficult to discern a pattern in the distribution of *Kofoidinium*. The highest abundance was only 4 specimens per sample (10 cells L^{-1}). In the Kuroshio Current and adjacent waters, the abundance was higher in summer than in spring (Figs 2, 3). Specimens of *Kofoidinium* were only found near the surface in the SE Asia marginal seas (Fig. 4), but in other waters they were found at depths down to 200 m. Overall, no clear longitudinal or vertical pattern in the distribution was observed, suggesting ubiquitous distribution of the organism in warm waters (Figs 2–6). The trophic conditions in these regions were described in Gómez et al. (2005). In the equatorial and southeast Pacific Ocean, the records of *Kofoidinium* tended to be more abundant in the most eutrophic regions, such as the vicinity of the Marquesas Islands and Peru-Chile Current (Fig. 6). In the Pacific Ocean the specimens were recorded in a wide range of temperature from 14 °C near the Chilean upwelling to 30 °C in equatorial surface waters (Figs 2–6).

Morphology of *Kofoidinium*

It is not easy to identify kofoidiniaceans to species due to the high morphological variability during their life cycle and the difficulties to delimit the species from preserved specimens. In the present study, the records of Kofoidinium have been tentatively grouped into four species: *Kofoidinium* sp., *K. velelloides* and *K. pavillardii* that are identifiable with more certainty and the more dubious *K. splendens*. The limits of this last taxon are unclear due to common morphological characters with the other species. In no case did preserved specimens of *Kofoidinium* retain the shell which is carried above the episome in life (see Cachon and Cachon 1967b).

The smaller specimens encountered ranged from 40 to 200 μm in diameter. The most extended morphology was a round to slightly elliptical to pentagonal flattened hyposome or ventral region, ranging ridges and bordered by a narrow differentiated band (Figs 7–10). The reduced episome formed a crest at the anterior margin of the cell. The nucleus was small and located in the episome. In the antero-dorsal margin appeared a short finger-like structure. The marginal differentiated band was thicker at the ends and in the antero-ventral region bifurcated forming a right angle. One extreme of this bifurcation of the marginal band was thick and formed a square-ended protrusion. The other branch was slightly curved and projected towards the episome (Fig. 7). One of the main characteristics of the Pacific specimens was the pointed extension that arises from the episome towards the ventral side of the cell. This pointed extension was flexible and tended to be in a different plane from the flattened hyposome (Figs 7 and 8). These small Pacific specimens that differed from the description of *K. velelloides* in Cachon and Cachon (1967b) are here named *Kofoidinium* sp. Specimens lacking the pointed extension, the square-ended protrusion and with a large nucleus located anteriorly in the hyposome (Fig. 10) were closer to *K. velelloides* as illustrated by Cachon and Cachon (1967b). Due to their transparency and small size, *Kofoidinium* sp. and *K. velelloides* could be more easily overlooked during sample analysis than the highly visible *K. pavillardii* (Figs 8, 9, 11–15).

Kofoidinium pavillardii is the largest species of the genus. The diameter was longer than 300 μm and reached 700 μm (Figs 8 and 11). The round hyposome occupied nearly all the cell body. The marginal hyaline band is interrupted at about 2/3 of the cell height with thicker end regions, especially the ventral one. More anteriorly than the ends of the marginal band are located two hook-shaped structures, the anchorage mechanisms that held the hemispherical transparent dome or shell (Figs 11 and 14). These delicate hyaline domes are easily detached from the cell and had presumably been lost. The ventral anchorage mechanism (Fig. 14) is bigger than the dorsal one (Fig. 11). The shape of the episome varied between the specimens, sometimes forming a prominent crest (Fig. 12), and in others more reduced (Fig. 11). The specimen in Fig. 12 has the shape of *K. pavillardii* as illustrated by Cachon

Figs 7–23. Photomicrographs of kofoidiniaceans, bright field optics. **7**, *Kofoidinium* sp. (0°, 165°W, 150 m depth) with anterior episome at the left, the hyposome at the right and the ventral projections at the top. **8-9**, *Kofoidinium pavillardii* (large cell) and *Kofoidinium* sp. (small cell) (0°, 170°E, 0 m depth); the inset in Fig. 8 shows the *Kofoidinium* sp. cell at a different focal plane. **10**, *K. velelloides*, note the prominent nucleus (0°, 160°E, 110 m depth). **11**, *Kofoidinium pavillardii*. See the ventral anchorage mechanism in the inset (34°15′N, 138° E, 150 m depth). **12–15**, *Kofoidinium pavillardii* (30°N, 138°E, 125 m depth). **13**, Detail of the dorsal margin of the hyposome. **14**, Detail of the antero-ventral region and the anchorage mechanism. **15**, Detail of the inclusions in the margin of the hyposome. **16**, *Kofoidinium splendens* (7°25′N, 121°12′E, 10 m depth). **17–21**, *K. splendens* with red inclusions (0°, 170°W, 80 m depth). **19**, Detail of the inclusions in the cell body. **20**, The arrows indicate the concentric ridges with red inclusions. **21**, Detail of red inclusions in the periphery of the hyposome. **22-23**, Unidentified pairs of kofoidiniaceans, probably stage "c" after binary fission (0°, 175°W, 30 m depth). **23**, Detail of the presumed symbiotic microalgae. AM = anchorage mechanism for shell; CR = concentric ridges; F = fibrils; PE = pointed extension; SQ = square-ended projection; TF = transverse flagellum. Scale bars = 50 μm.

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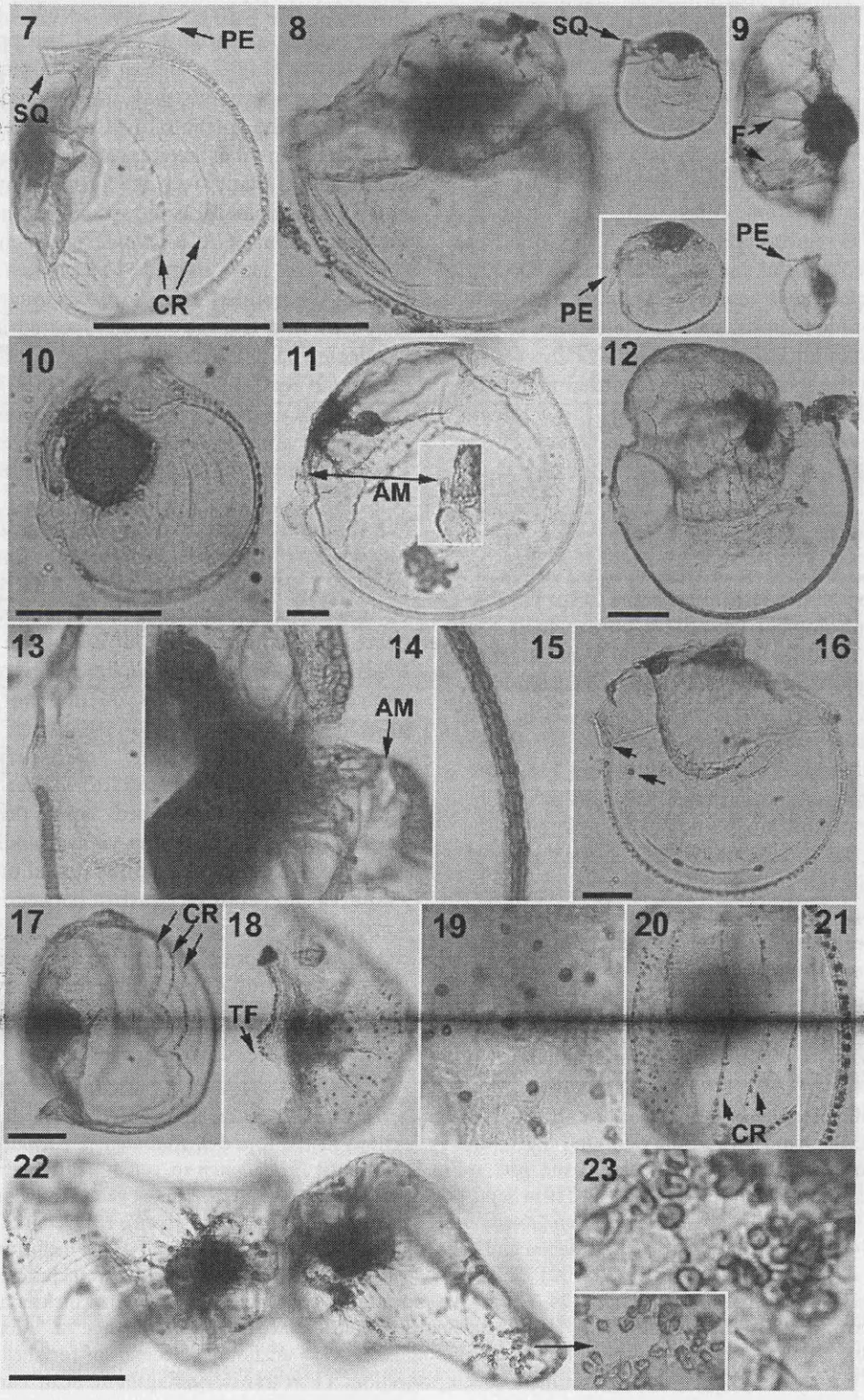
While the identification of *K. velelloides* and *K. pavillardii* is relatively easy, the determination of diagnostic characters of *K. splendens* and its validity as a species require further research (Fig. 13). Specimens >200 μm (usually 300–400 μm) with a smoothly rounded left cingular crest have been considered as *K. splendens* (Figs 16–21). Cachon and Cachon (1967b) considered that body inclusions are characteristic of *K. splendens*. However, the specimen of Fig. 12, whose shape resembled *K. pavillardii*, had a differentiated band



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filled with brownish granules (Figs 13 and 15). The specimens that harbour body inclusions in the margin of the hyposome, and also in the concentric ridges or dispersed over the cell body are here assigned to *K. splendens* (Figs 16–21). According to Cachon and Cachon (1967b) these red body inclusions in the Lugol-fixed specimens are of polypeptide nature rather than lipid bodies; thus, the possibility of that these red inclusions are symbiotic microalgae may be discarded. In the present study no symbiotic microalgae were observed in mature stages of *Kofoidinium*.

No noctilucacean species has been reported to have chloroplasts (excluding chloroplasts of the ingested prey or symbiotic microalgae). Tentative symbiotic microalgae were observed in an unidentified kofoidiniacean (Figs 22 and 23). This observation was made in a pair of recently divided cells. According to Cachon and Cachon (1967b) such reproduction by bipartition is restricted to the immature cells. The presumed symbiotic microalgae were distributed along tracts and showed an ellipsoidal to rotund shape and were 5–7 μm in diameter (Fig. 23). At the same sampling station, structures that appeared to be symbiotic microalgae were found in an unidentified immature stage (Figs 24 and 25).

Distribution and morphology of *Spatulodinium*

Spatulodinium pseudonoctiluca has the shape of a disc, about 100–120 μm in diameter, which has been deformed into a shallow cone by pushing in the left side so that the right side has become somewhat convex. A net of fibrils (Fig. 33) is thought to facilitate the ingestion of the prey of these heterotrophs. The main characteristic of the genus is the occurrence of a long unstriated movable tentacle projecting from the ventral side in the anterior part of the cell (Figs 26, 28–32). It is true that *Kofoidinium velelloides* (Fig. 7) and other unidentified kofoidiniaceans (Fig. 39) also have tentaculoid projections, but these differ in size or origin. Only one specimen with the morphology reported for the type species was encountered (Fig. 29). *Spatulodinium* was previously regarde as a monot ic genus onl kn wn from boreal-arctic waters from Europe to the Japan Sea. The specimen identified as *Spatulodinium pseudonoctiluca* from the Peru-Chile Current constitutes the first record of this genus in the southern hemisphere (Fig. 29).

Beyond the type species, other specimens that differed from the type of *Spatulodinium* were observed. Three specimens corresponded to a large cell (~150 μm diameter) with a long tentacle and showing a green pigmentation (Figs 26–28). In SE Asia marginal seas, only one mature specimen was recorded in the open waters of the Sulu Sea (Figs 26 and 27). Two other specimens of "green" *Spatulodinium* sp. 1 were observed in the western and central equatorial Pacific Ocean (Fig. 28). The tentacle was very long in one of the specimens (two times the cell body, Fig. 26) and shorter and with a pointed-ending in the other specimen (Fig. 28). In these "green" *Spatulodinium* sp. 1 the typical system of fibrils was not visible or was masked by the green pigmentation (Figs 27 and 28).

Other unidentified species of the genus were observed with two different morphologies. The tentacle of the type species projected from the antero-ventral region. In these other specimens the tentacle appeared to project from the posterior part of the cell. Several specimens of *Spatulodinium* sp. 2 were about one half (~50 μm) of the diameter of the type species and showed a thick tentacle with a triangular transparent halo (Fig. 30). Specimens of *Spatulodinium* sp. 3, also of smaller size than the type species, showed a *Daphnia*-like shape, with a clearly visible flagellum (Figs 31 and 32).

The highest abundance of *Spatulodinium* spp. with 7 specimens was encountered in a eutrophic region near the Juan Fernández Archipelago, associated with a surface proliferation of *Gonyaulax polygramma* Stein. Also immature life stages which have been described as *Gymnodinium pseudonoctiluca* (Fig. 33) and *Gymnodinium lebouriae* (Fig. 34), precursors of mature stages of both *Spatulodinium* and *Kofoidinium*, were found at the same station. Consequently these immature stages cannot be strictly ascribed to *Spatulodinium* because specimens of *Kofoidinium pavillardii* were also observed

Figs 24–41. Photomicrographs of kofoidiniaceans, bright field optics. **24-25**, Tentatively identified as the immature stage of a kofoidiniacean with a green pigmentation (0°, 175°W, 60 m depth). **26-27**, "Green" *Spatulodinium* sp. 1 (7°25′N, 121°12′E, 75 m depth); inset shows the same cell in a different orientation. **27**, Detail of the green pigmentation of the same cell as in Fig. 26. **28**, "Green" *Spatulodinium* sp. 1 (0°, 160°E, 40 m depth). **29**, *Spatulodinium* cf. *pseudonoctiluca* (31°54′S, 91°27′W, 5 m depth). **30**, *Spatulodinium* sp. 2 with a tentacle that is thicker in the proximal part (33°22′S, 78°6′W, 40 m depth). **31-32**, "*Daphnia*-like" *Spatulodinium* sp. 3 with a tentacle that projects from the posterior episome region. **31**, Specimen from 31°54′S, 91°27′W, 40 m depth. **32**, Specimen from 33°22′S, 78°6′W, 5 m depth. **33**, Stage "c" of a kofoidiniacean described as *Gymnodinium pseudonoctiluca* (33°22′S, 78°6′W, 15 m depth). **34**, Stage "d" described as *Gymnodinium lebouriae* (33°22′S, 78°6′W, 5 m depth). **35**, Tentatively identified as *Pomatodinium* sp. (33°N, 138°E, 60 m). **36–38**, Unidentified kofoidiniacean (32°N, 138°E, 100 m). Figs 36 and 37 resemble illustrations of *Pomatodinium impatiens* in the description by Cachon and Cachon-Enjumet (1966); note the prominent fibrils. **39–41**, Unidentified kofoidiniacean with two long tentacles emerging from the margin of the hyposome, one smaller tentacle and a prominent anterior crest (0°, 180°, 200 m depth); note the concentric areolation in Fig. 40. C = cingulum; F = fibrils; L = left side; R = right side; S = sulcus; T = tentacle; TF = transverse flagellum. Scale bars = 50 μm.

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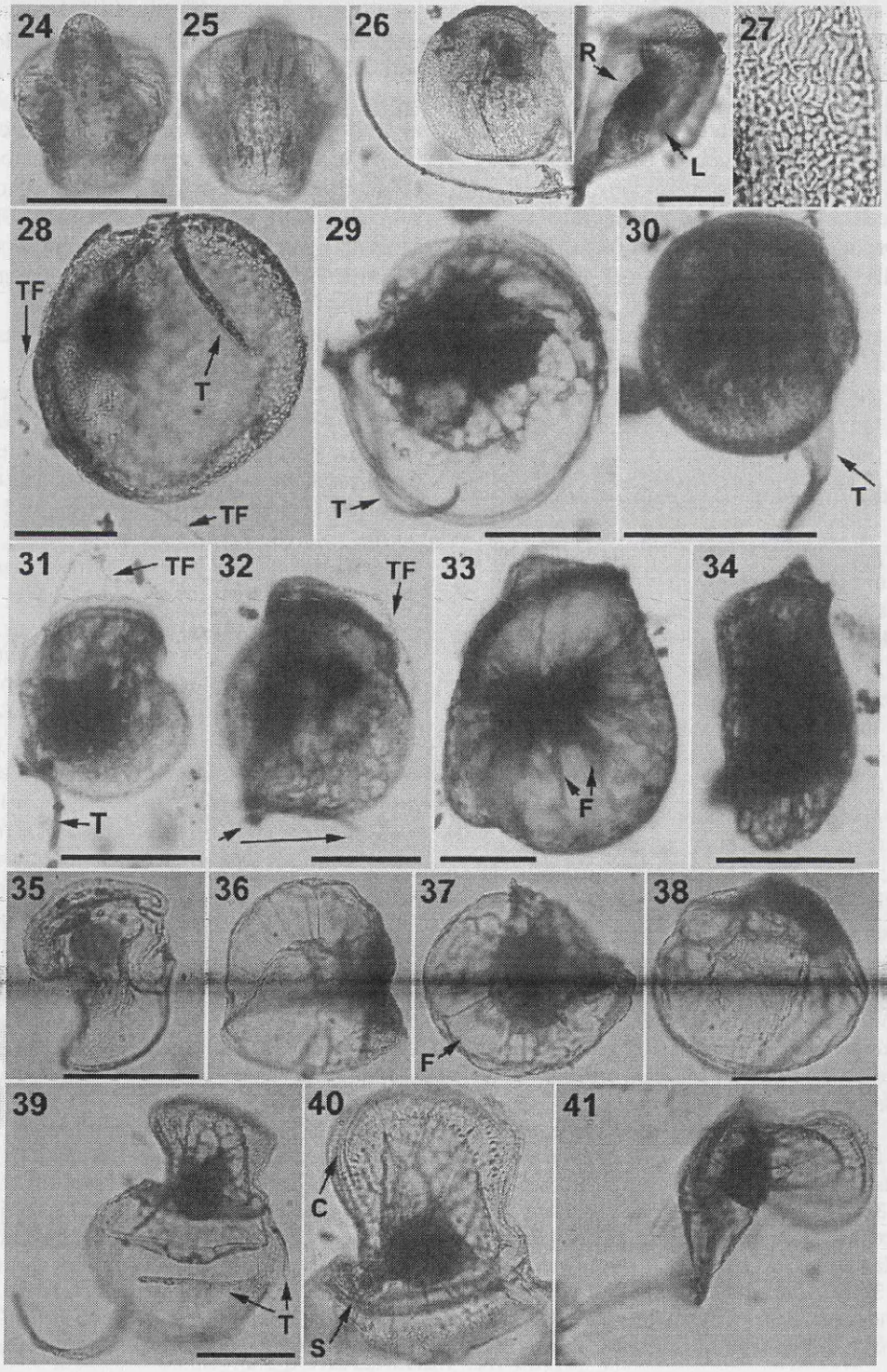
in the same location.

Morphology of other kofoidiniaceans

Cachon and Cachon-Enjumet (1966) described the shape of *Pomatodinium* as resembling a gastropod larva, but with changes of shape due to the contraction of fibrils (like those found in *Kofoidinium*, see Fig. 9); they also reported that it may contain symbiotic microalgae. They illustrated *Pomatodinium* from a few live specimens, but found the morphology varied among fixed specimens. One specimen found by us in the Kuroshio



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region is assumed to belong to the genus *Pomatodinium* (Fig. 35).

Another specimen was composed of two hemispherical transparent domes, one inside the other, and joined at their rims. An inner net of fibrils joined the two hemispherical domes. One of the views of the specimen (Fig. 37) was similar to the figure "d" of *Pomatodinium impatiens* in Plate I by Cachon and Cachon-Enjumet (1966). However in other views the morphology of the specimen differed from the description of *Pomatodinium*. In one view the specimen had the shape of a Roman Centurion's helmet with the nucleus located in one side of the crest (Fig. 36). In one view the specimen could be mistaken for *Kofoidinium* (Fig. 38) and provides a clear example of the need to view kofoidiniaceans from different orientations to understand their true shape.

Another unidentified kofoidiniacean (~110 μm long) showed a very distinctive shape and extensions (Figs 39–41). The nucleus was located at the base of the episome (Fig. 40). A semicircular crest with a concentric inner areolation was observed in the episome (Fig. 40). The cingulum extended along the marginal part of the crest and the sulcus along the base of the crest (Fig. 40). The margin of the hyposome did not show the differentiated band that characterises *Kofoidinium*. The specimens showed three tentaculoid extensions from the hyposome, each with rounded-tips (Figs 39 and 41). The longer extension projected from the postero-ventral part of the margin of the hyposome. At the opposite side, slightly anteriorly, emerged another long extension (Fig. 39). These extensions originated from a different position compared with the single tentacle of *Spatulodinium*. A third short finger-like extension was visible emerging from the anterior-dorsal margin of the hyposome (Fig. 39).

Discussion

How many species of *Kofoidinium*?

The existing literature on the life cycle of kofoidiniaceans is restricted to Cachon and Cachon (1967b) and Konovalova and Selina (2002), and has been largely overlooked. When Pavillard (1921) reported *Gymnodinium pseudonoctiluca* in the NW Mediterranean Sea, he was probably illustrating stage "c" of *Kofoidinium*. Later, Pavillard (1928) found the mature stage and described *Kofoidinium velelloides*; he misspelled the epithet 'velleloides' that refers the jellyfish *Velella velella* Linnaeus, but subsequently corrected it (Pavillard 1937). Pavillard (1928) reported that the size of *K. velelloides* was 350 μm long. However as reported by Cachon and Cachon (1967b) and the present study, the size of *K. velelloides* was usually less than 200 μm. This confusion may be responsible for the fact that no new species was described until 1967 and all the previous records of large specimens of *Kofoidinium* were ascribed to *K. velelloides* (Balech 1962; Fenaux 1958; Halim 1967; Rampi 1952). The description of *K. splendens* by Cachon and Cachon (1967b) did not provide sufficient definitive criteria to differentiate it from *K. velelloides*. The system of anchorage of the dome is different, but this morphological character is difficult to observe (Fig. 14). A high confusion exists in the literature. For example in the British Isles, Parke and Dodge (1976) listed *K. splendens* and no *K. velelloides* and later Dodge (1982) reported only *K. velelloides*. For *Kofoidinium splendens* Taylor (1976, p. 185) reported "*Precise distinctions between this species and K.– velleloides – Pavillard are difficult to make because of the incompleteness of the original description and the distorted condition of the type specimens of the latter*". Cachon and Cachon (1967b) reported that *K. splendens* may harbour several symbiotic zooxanthellae that are lost under eutrophic conditions as well as the red polypeptide bodies. This variability does not help in differentiating *K. splendens* from *K. velelloides*.

Cachon and Cachon (1967b) already reported specimens of *K. velelloides* of about 100 μm in length. Nearly all the previous studies that reported kofoidiniaceans were based on net sampling and subsequently these small specimens could be lost. In addition, some specimens may be overlooked during routine microscopical analysis due to their small size and transparency. In the present study specimens of *Kofoidinium* sp. 40 μm in diameter were commonly observed. The pointed extension and the square-ended protrusion (Fig. 7) are distinctive characters that were clearly lacking in *K. velelloides* (Fig. 10).

Bursa (1964) described *Kofoidinium arcticum* in the Canadian arctic waters. Cachon and Cachon (1967b, p. 437) and Taylor (1976, p. 184) reported that *K. arcticum* is a doubtful taxon, which was described from a single formaldehyde-fixed specimen evidently deformed due to preservation. Beyond the initial description no records

Kofoidinium splendens can be also confused with *K. pavillardii*. Both species have similar system of anchorage of the dome (Cachon and Cachon 1967b). According to Taylor (1976) *Kofoidinium lebouriae*, usually misspelled as 'lebourae', is the correct name for *K. pavillardii* because *Gymnodinium lebouriae* is considered as the basionym. Cachon and Cachon (1967b) stated that *Gymnodinium lebouriae* is stage "d" of a kofoidiniacean and consequently it is not a valid species, which added more confusion. For example Yamaji (1980, p. 107) reported the non-existent species names "*Kofoidinium lebourae* (Pavillard) Cachon et

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Cachon" or considered *Kofoidinium splendens* as a synonym of *Kofoidinium lebouriae*.

The observations of the present study suggest the existence of a small species with a pointed extension, here called *Kofoidinium* sp. (Fig. 7), *K. velelloides* (Fig. 10), a large species, *K. pavillardii* (= *K. lebouriae*) (Fig. 11) and a fourth species, *K. splendens* (Fig. 17), of more uncertain delimitation.

How many species of *Spatulodinium*?

Spatulodinium is a monotypic genus, only known from northern hemisphere Euro-Asian boreal and arctic waters. This study is the first to describe the genus *Spatulodinium* in tropical waters and in the southern hemisphere. In addition to the specimens with a green pigmentation that suggests the occurrence of chloroplasts (Figs 32–35), other specimens that differed from the type species were found (Figs 37–41). The monotypic character of the genus needs to be reconsidered.

In European Atlantic waters, immature stages presumed to belong to the genus *Spatulodinium* have been described as *Gymnodinium lebouriae*, *G. fulgens* and *G. conicum* (= *G. viridis*), as well as probably *G. pyrocystis* that was described with no illustration (Kofoid and Swezy 1921). In the tropical and southern Pacific Ocean, these immature stages were observed as well as other unidentified kofoidiniaceans. Kofoid and Swezy (1921) described *Amphidinium vasculum* and *A. pacificum* in tropical waters of the Eastern Pacific Ocean. These forms strongly resemble the stage "d" of a kofoidiniacean (Fig. 34). The suggestion that these large *Amphidinium* species, described from single specimens, could correspond to immature stages of *Spatulodinium* in tropical waters, cannot be discarded.

Other species of kofoidiniaceans

As well as *Kofoidinium* and *Spatulodinium*, the genera *Pomatodinium* and *Cymbodinium* have been included in the family Kofoidiniaceae. One of the specimens observed in the Pacific Ocean was described as *Pomatodinium* (Fig. 35) and another specimen resembles that genus in one or two views (Fig. 37). Beyond the type locality, the Ligurian Sea, *P. impatiens* was reported from Spanish Mediterranean coasts (Margalef 1969) and the NE Atlantic Ocean (Travers and Travers 1975; Margalef 1975). In the Pacific Ocean, Sakka et al. (2002) reported *Pomatodinium* as a dominant species in an atoll lagoon in French Polynesia, but this record is questionable.

The genus *Cymbodinium* J. Cachon et M. Cachon is the least known kofoidiniacean. *Cymbodinium* was described from the coastal Ligurian Sea (Cachon and Cachon 1967b); it was further reported with no illustration from NE Atlantic waters (Parke and Dodge 1976) and an estuary in Brazil (Bergesch and Odebrecht 1997). No information on the appearance of fixed specimens of *Cymbodinium* exists. These specimens may be too distorted by fixation to be identified.

The noctilucaceans are of great interest in the phylogenyn of dinoflagellates. However, the existing phylogenetic information is restricted to *Noctiluca* (Taylor 2004). Most of the species of kofoidiniaceans were previously described from the NW Mediterranean Sea. The present study reveals that there is an extensive but almost unknown diversity of noctilucaceans in the oceans of the world.

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On the ecology and unusual life cycle of the dinoflagellate *Spatulodinium pseudonoctiluca* in the NE English Channel

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Abstract

The distribution of *Spatulodinium* (=*Gymnodinium*) *pseudonoctiluca* (Pouchet) J. Cachon *et* M. Cachon has been investigated for 8 years (1998-2005) in the NE English Channel, type locality of the species and its immature stages. The species can be found after the spring diatom bloom from late May to October. The highest abundance was found in June 2004 after the *Phaeocystis* bloom. Exceptionally, the *Phaeocystis* bloom was absent in 2005 and only several specimens of *S. pseudonoctiluca* were observed. The immature and mature stages of *Spatulodinium* nearly always co-occurred. No other kofoidiniaceans such as *Kofoidinium* or *Pomatodinium* were observed. The first stages of the development of *Spatulodinium* can easily confuse with gymnodiniaceans. The transformation of the stage "D", which has been described as *Gymnodinium lebouriae* (=*G. fulgens*) or *Gymnodinium conicum* (=*G. viridis*), into the mature stage, is illustrated. The stage "D" is originated from a cluster of pairs of smaller cells joined by an elongate episome. In the oriental Atlantic Ocean, *Spatulodinium pseudonoctiluca*, a single species which life stages are often reported as separate species, is especially adapted to a strongly fluctuant environment.

Résumé

Sur l'écologie et le cycle de vie peu commun du dinoflagellé *Spatulodinium pseudonoctiluca* dans la Manche orientale.

Durant 8 années (1998-2005) la distribution de *Spatulodinium* (=*Gymnodinium*) *pseudonoctiluca* (Pouchet) J. Cachon *et* M. Cachon a été étudiée dans la Manche Orientale qui est un environnent type de cette espèce et de ses stades de développement. *S. pseudonoctiluca* peut y être observée après le bloom printanier des diatomées de fin mai jusqu'à octobre. Son abondance la plus élevée a été mesurée en juin 2004 après le bloom de *Phaeocystis*. En 2005 le bloom de *Phaeocystis* était exceptionnellement absent et seuls plusieurs spécimens de *S. pseudonoctiluca* ont été observés. Les stades de développement immature ainsi que le stade adulte de *Spatulodinium* apparaissent souvent en même temps. Aucune autre kofoidiniacea telle que *Kofoidinium* ou *Pomatodinium* n'a été observée pendant cette période. Les premiers stades de développement de *Spatulodinium* peuvent facilement être confondus avec des gymnodiniaceas. La transformation du stade "D", décrite comme étant le stade immature de *Gymnodinium lebouriae* (=*G. fulgens*) ou de *Gymnodinium conicum* (= *G. viridis*), en stade adulte est ici illustrée. Le stade "D" provient d'un faisceau de paire de petites cellules jointes par un episome allongé. Dans l'Océan Atlantique boréal, *Spatulodinium pseudonoctiluca*, une espèce unique dont les stades de développement sont souvent décrit comme étant des espèces différentes, est particulièrement adapté à un environnement fortement fluctuant.

Keywords: Spatulodinium pseudonoctiluca; *Gymnodinium lebouriae* lebouriae; Dinoflagellate; Life cycle; Microbial ecology

Mots-clés: Spatulodinium pseudonoctiluca; *Gymnodinium lebouriae* lebouriae; Dinoflagellé; Cycle de vie; Écologie microbienne

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1. Introduction

The members of the family Kofoidiniaceae F.J.R. Taylor undergo an exceptional morphological transformation during their life cycle. This is responsible of the confusion on the identification of the species of the kofodiniaceans. In one of the earlier works on marine dinoflagellates, Pouchet described *Gymnodinium pseudonoctiluca* from the coast of Brittany, SE English Channel [1]. Pouchet found intermediate characteristics between gymnodiniaceans and *Noctiluca scintillans* (Macartney) Kofoid. The two flagella, the occurrence of the cingulum and the sulcus is reminiscent of the gymnodiniaceans, especially the immature stage with an anterior cingulum that resembles a large *Amphidinium*. The surface of the cell and the radiating fibrils from the perinuclear region resembles *N. scintillans* [1]. Pouchet illustrated *G. pseudonoctiluca* as a single species with two different forms. One form corresponded to a large *Amphidinium*-like pigmented and the other form, the mature stage, was a round or oval non-pigmented laterally compressed cell.

Off Plymouth (SW English Channel), near the type locality of *G. pseudonoctiluca*, Lebour found 3 specimens of the immature stage of *G. pseudonoctiluca* [2]. From a single highly pigmented specimen, she described *Gymnodinium viridis* Lebour [2]. Kofoid and Swezy realized that the species name *G. viridis* was already occupied and they proposed *G. conicum* Kofoid *et* Swezy [3]. They considered that Pouchet was mistaken two species as a single one [3, p. 244]. They considered that one of the immature stages of *G. pseudonoctiluca* in Lebour [2] was a separate species. They proposed *Gymnodinium fulgens* Kofoid *et* Swezy based on the Lebour's figure. Pavillard observed immature stages of kofoidiniaceans in the NW Mediterranean Sea [4]. He considered that these forms, similar to the records by Pouchet and Lebour of *G. pseudonoctluca*, corresponded to a separate species and Pavillard proposed *Gymnodinium lebouriae* [4] (orignally described as 'lebourii' and commonly misspelled as 'lebourae'; ICBN: Art. 60.11; Ex. 24.; Recom. 60C.1.b; Art. 23.5 and 32.5; [5]). Later, Pavillard described the type species of *Kofoidinium* that at a first sight mainly differed from mature stage of *G. pseudonoctiluca* in the lack of the tentacle [6].

Cachon and Cachon investigated their

collected from the coastal Ligurian Sea (NW Mediterranean) [7]. They recognized six sages labelled from "A" to "F". The morphology of the immature stages of the kofoidiniaceans was too similar to distinguish and the species could only be identified at the sporont stage. In the stage "A" and "B", the spores first develop into *Gymnodinium*-like ovoid motile cells (<35 μm long), which resemble non-pigmented gymnodiniaceans. As this stage, the cells ingest small particles such as bacteria. In stage "C", the hyposome has a globular shape and the cells develop a structure of fibrils radiating from the perinuclear region resembles *N. scintillans*. This stage was illustrated as *G. pseudonoctiluca* in Pouchet [1] and Pavillard [4]. Stage "D" has received the names *Gymnodnium*

lebouriae (=*G. fulgens*) and *G. conicum* (=*G. viridis*). In this stage, the globular hyposome transforms into a cylindrical shape that resemble a large *Amphidinium*-like cell. The shape of the episome is highly variable and sometimes a peduncle is observed. The cell develops a marked net of fibrils towards the cystostome and is able to ingest larger particles such as diatoms and silicoflagellates. At this stage, the cells reach the higher degree of pigmentation. According to Cachon and Cachon due to small pigmented lipid droplets and chloroplasts were not observed in any of the life stages [7]. In stage "E", after the cells get the higher biomass, the cells transform into the sporont flattening laterally (stage "F"). The differences in the morphology of the mature specimens allow the identification of the specimens to species. In the case of mature *Spatulodinium* a tentacle is projected from the ventral region.

The distribution of the kofodiniaceans is mainly restricted to warm to tropical waters, with the exception of *Spatulodinium* (=*Gymnodinium*) *pseudonoctiluca* only known from boreal waters and from the northern Mediterranean [7,8,9] and the Black Sea [10]. In the eutrophic and turbulent waters of the English Channel, the dinoflagellate assemblage has a low diversity. However, after the spring *Phaeocystis* Lagerheim and diatom bloom, *S. pseudonoctiluca* and its life stage "D" misidentified as *G. lebouriae* and *G. viridis* are highly distinctive species [1,2]. The present study investigated the seasonal and interannual distribution of the life stages of *Spatulodinium*, often considered as separate species, during 8 years in the proximity of the type locality. Illustrations of the transformation from stage "D" into the mature stage are provided. This study is the first to describe an unusual reproductive stage in *Spatulodinium* that consisted of a cluster of pairs of small cells that were similar in form to the previously described species *G. lebouriae*.

2. Material and methods

Within the context of the SOMLIT monitoring program (Service d'Observation en Milieu LITtoral) 127 cruises were carried on board R/V *Sepia II* from November 1997 to December 2005 off Boulogne-sur-Mer (NE English Channel). Two permanent stations were sampled during the high tide. One station was located at 2 Km offshore (50°40'75N; 1°21'17E; 21 m depth) and other station was located at 8 Km offshore (50°40'75 N; 1°24'60 E, 50 m depth). The sampling frequency was planned to be biweekly, but cruises were often cancelled or were restricted to the most coastal station due to meteorological constraints. During the spring and summer of 2003, 2004 and 2005, additional cruises were carried out with a sampling frequency planned to be once a week. Seawater samples were collected with a Niskin bottle at the surface and the bottom. Lugol-fixed samples of 25 or 50 mL were settled in composite settling chambers. The entire chamber was scanned at 200× with an IX71 inverted Olympus microscope equipped with an Olympus digital camera and each specimen was photographed at 400× with the DP70-BSW software.

3. Results

3.1. Temporal distribution in the NE English Channel

Spatulodinium was observed from May to October each year from 1998 to 2005 (Fig. 1). The highest abundance, 320 cells L^{-1} (8 specimens in 25 mL) was observed in June 2004 after the bloom of *Phaeocystis* and diatoms, mainly *Guinardia delicatula* (Cleve) Hasle. Anomalously in spring 2005, the bloom of *Phaeocystis* spp. was not observed and only one specimen of *Spatulodinium* was observed. The abundance of microplankton as well as *Spatulodinium* was higher in the coastal stations. No clear differences in the vertical distribution of *Spatulodinium* were observed in this highly turbulent environment. During and after the spring *Phaeocystis*-diatom bloom, the dinoflagellate assemblage showed a low diversity. Heterotrophic species such as *Gyrodinium spirale* (Bergh) Kofoid *et* Swezy and *Protoperidinium* spp. were dominant. The only noctilucacean observed was the distinctive sporont of *Spatulodinium* and its immature stages, with the exception of a very few records of *Noctiluca scintillans*.

3.2. Morphology and life stages

The mature specimens of *S. pseudonoctiluca* (80-180 μm long) tend to be more oval than rounder in shape. The elongate tentacle was observed in all the specimens (Figs 11-14). The undulate flagellate often appeared unattached (Figs 12-13). Stage "D", precursor of the mature stage, was the most distinctive of the immature stages and co-occurred with the sporont in nearly all the samples. This form, described as *Gymnodinium lebouriae*, showed a cylindrical shape with an anterior cingulum that resembles a large highly pigmented *Amphidinium*-like cell (Figs 6-10). One of the specimens showed two small "wings" during the transformation from stage "D" into the sporont *Spatulodinium* (Fig. 9). Coinciding with the period of highest abundance of *Spatulodinium* in June 2004, a cluster of four pairs of smaller cells of the form *G. lebouriae* joined at the elongate episome was observed (Figs 4-5). This may be the origin of the elongate episome observed in stage "D" (Fig. 6). Also, co-occurring with the p

visible net of fibrils was observed. These cells, with variable degrees of pigmentation, may correspond to stages "B" or "C" of *Spatulodinium* (Figs 2-3). In the case of other smaller *Gymnodinium*-like cells, it is difficult to discern if they are gymnodiniaceans or immature stages ("A", "B") of *Spatulodinium*.

4. Discussion

4.1. Distribution in boreal-Arctic waters.

The complex morphological transformation along the life cycle is responsible of the confusion in the identification of the species of kofoidiniaceans. The morphology of the immature stages of *Spatulodinium* and *Kofoidinium* are so similar that it is difficult to identify the genera to which the immature specimens belong.

Spatulodinium pseudonoctiluca has been reported along the boreal Atlantic European waters, Russian and Canadian Arctic waters and in the vicinity of the Japan Sea [11]. However in several checklists in the Atlantic European waters *Spatulodinium* (=*Gymnodinium*) *pseudonoctiluca* and *G. lebouriae* are both included as separate species [12,13,14,15,16]. In British waters, Dodge considered *G. lebouriae* an immature life stage of *Kofoidinium* [13]. If this consideration is valid, *Kofoidinium* should appear associated with *G. lebouriae* in the English Channel. However the only species co-occurring with *G. lebouriae* is *Spatulodinium*. All the species, *G. pseudonoctiluca*, *G. lebouriae* and *G. viridis* were described in the English Channel in June or July, which is the period of higher abundance of *Spatulodinium* as reported in the present study. No species of *Kofoidinium* have been reported in the boreal Atlantic Ocean [15,16], Russian Arctic waters [17] or the Japan Sea [18], with a very few exceptions west Ireland [19] and the Norwegian Sea [13, 20]. Bursa [21] described *K. arcticum* in the Canadian Arctic waters where *G. pseudonoctiluca* has been reported [22]. As reported by Cachon and Cachon [7, p. 437] and Taylor [23] *K. arcticum* is a doubtful taxon, described from a single fixed specimen evidently deformed due to the preservation. Records of *Kofoidinium* in very cold waters of high latitudes are very rare compared to the more common *Spatulodinium*.

4.2. Records beyond boreal-Arctic waters

The records of *Kofoidinium* in the boreal-Arctic waters are rare. However, *Kofoidinium* is common in the Mediterranean Sea [23], whereas the records of *Spatulodinium* are scarce. Cachon and Cachon illustrated the sporont in the Ligurian Sea [7]. In the Adriatic Sea, both *Spatulodinium* and *Kofoidinium* have been listed [8,9] as well as *G. pseudonoctiluca* and *G. lebouriae* [25]. The distribution of *Kofoidinium* and *Spatulodinium* overlaps in the colder basins of the Mediterranean Sea. In the Black Sea, the only record of *S. pseudonoctiluca* corresponds to Stoyanova [10]. No records of *Kofoidinium* exist in the Black Sea [26].

The records of *Kofoidinium* in temperate to tropical waters are numerous [23] and its immature stages may be referred as *G. pseudonoctiluca* [27,28]. Following Cachon and Cachon [7], Balech illustrated stage "C" of *Kofoidinium pavillardii* as *G. pseudonoctiluca* [27]. He reported *K. pavillardii* and *K. velelloides* and he did not find *S. pseudonoctiluca*.

4.3. Ecological aspects

The NE English Channel, near the Strait of Dover, is a shallower environment subjected to intense winds and a tidal flux of 8 meters [29]. A bloom of *Phaeocystis* dominates this highly turbulent environment in spring and diatoms throughout the year. The early immature stages of *Spatulodinium* feed on small particles such as bacteria, whereas the large stages, especially stage "D", feed on larger particles such as diatoms. The *Phaeocystis* post-bloom conditions, usually around June, provide abundant detritical material from the decomposition of *Phaeocystis* that may favour the development of immature stages. The present study for the first time illustrates a unique reproduction of the immature stage "D" (Figs 4-5). Cachon and Cachon observed an 8-cell chain that in only 2 hours divides into a 16-cell chain [7]. Stage "D" seems to develop a strategy of fast division in the short period of favourable conditions. The high abundance of diatoms in late spring and early summer is the source of preys for the larger stages of *Spatulodinium*.

The present study investigates for the first time the ecological distribution of members of the family Kofoidiniaceae. *Spatulodinium* is especially adapted to the strong phytoplankton fluctuations in the turbulent northern English Channel. The unique mechanism of reproduction, which is here for the first time illustrated, facilitates the fast division and the occurrence of the mature stage in the short period of favourable conditions.

Acknowledgements

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Figure legends

Fig. 1. Temporal distribution of the abundance (cell L^{-1}) of *Spatulodinium pseudonoctiluca* in the NE English Channel off Boulogne-sur-Mer from 1998 to 2005.

Figs 2-14. Photomicrographs of *Spatulodinium pseudonoctiluca*. 2-3. Stage "C", usually reported as *Gymnodinium pseudonoctiluca*. 4-5. Cluster of pairs of small cells of stage "D". 6-10. Stage "D", usually reported as *Gymnodinium lebouriae* (=*G. fulgens*) or *G. viridis* (=*G. conicum*). The arrows in fig. 9 indicate to two twin transformation from stage "D", *G. lebouriae*, into the mature stage. 11-14. Mature specimens. The arrows indicate the undulate flagellum. Scale bar =50 µm.

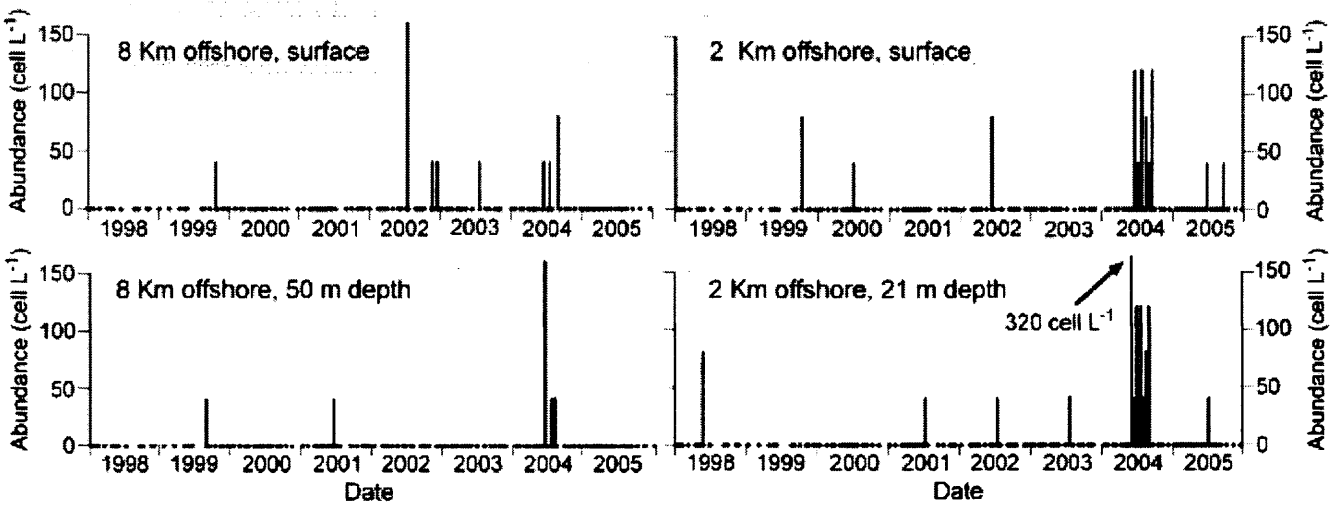
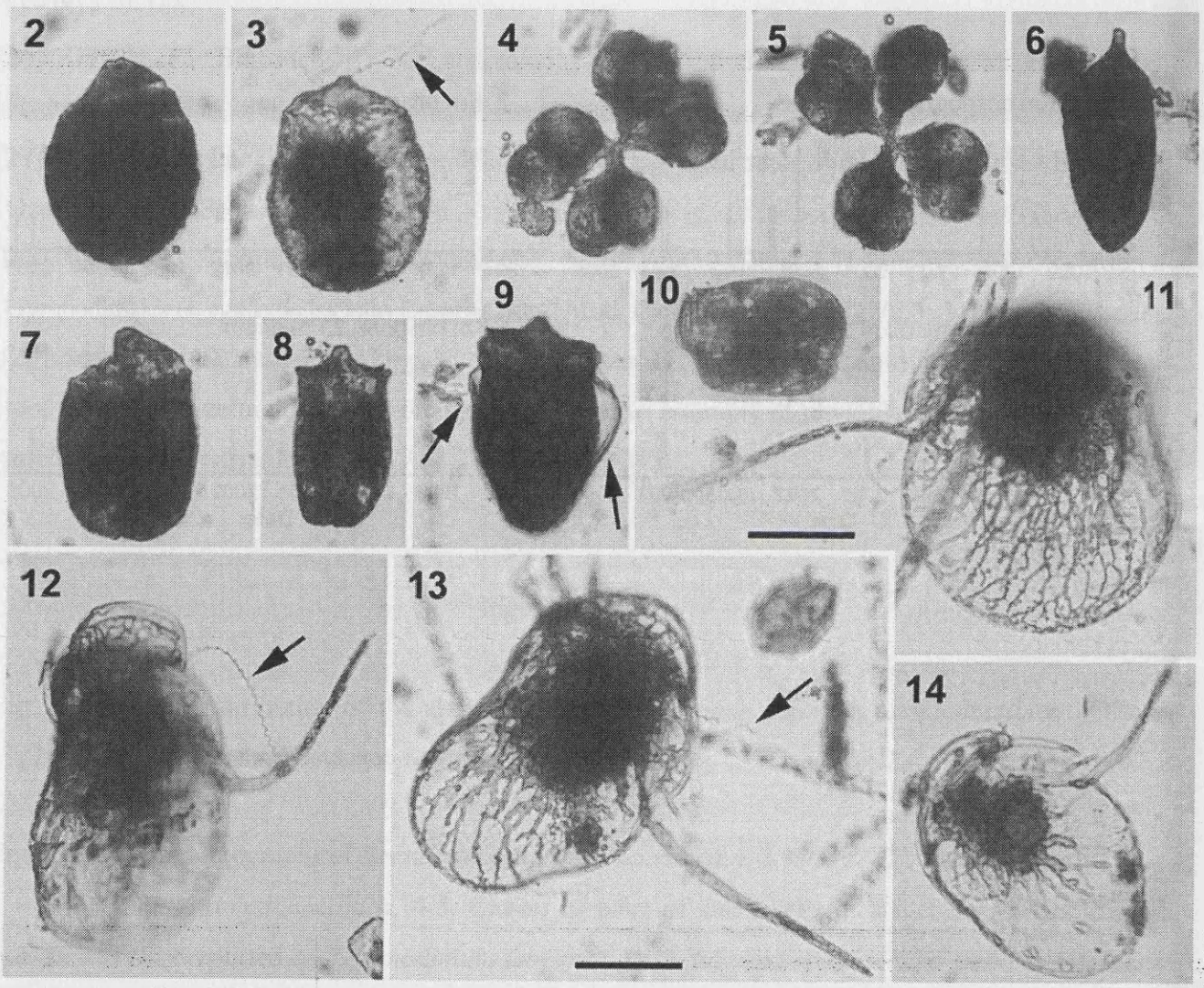

8 Km offshore, surface
2 Km offshore, surface
8 Km offshore, 50 m depth
2 Km offshore, 21 m depth
320 cell L-1
Abundance (cell L-1)
Date
0
50
100
150
1998
1999
2000
2001
2002
2003
2004
2005

Fig. 1.



Figs 2-14

3.2. Taxonomía y distribución de dinoflagelados poco conocidos:

3.2.5. Dinophysiales: *Histioneis*

Gómez, F., 2005. *Histioneis* (Dinophysiales, Dinophyceae) from the western Pacific Ocean. *Botanica Marina* 48, 421-425.

Gómez, F., 2007. Synonymy and biogeography of the dinoflagellate genus *Histioneis* (Dinophysiales, Dinophyceae). *Revista de Biología Tropical* 55, aceptado.

Histioneis (Dinophysiales, Dinophyceae) from the western Pacific Ocean

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Abstract

The distribution of the dinoflagellate *Histioneis* was studied in the vicinity of the Kuroshio Current, the Philippine, Celebes, Sulu and South China Seas and the western and central equatorial Pacific Ocean. A total of 65 specimens, assigned to 17 species, was observed. For the first time, photomicrographs of several species are reported. *Histioneis cymbalaria* and *H. longicollis* were the most common. Nearly all specimens were recorded from 0–70 m depth, and the highest abundance was recorded in the Philippine Sea in July (32°N, 138°E, 30 m depth) with a maximum of 32 individuals per litre.

Keywords: dinoflagellates; Dinophysiales; *Histioneis*; Pacific Ocean; phytoplankton.

Introduction

The tropical dinophycean *Histioneis* Stein (Histion=wing, neis=vessel) is characterized by an antero-posteriorly flattened, usually rotund to reniform or subreniform cell body with ornate hyaline list and rib systems. The left sulcal list is highly developed, whereas the right sulcal list is vestigial. The cingulum has a very long dorsal edge, is almost horizontal, and very concave. The epitheca has been reduced to a minute disc (Kofoid and Skogsberg 1928). Chloroplasts are absent and symbiotic cyanobacteria occur between the two robust lists of a large cingular chamber (Hallegraeff and Jeffrey 1984). The genus *Parahistioneis* Kofoid *et* Skogsberg is distinguished from *Histioneis* mainly by the absence of the submarginal cross-rib of the posterior cingular list found in *Histioneis* (Kofoid and Skogsberg 1928). *Parahistioneis*, intermediate between the genera *Ornithocercus* Stein and *Histioneis*, is considered to be congeneric with *Histioneis* (Balech 1971, 1988, Sournia 1986).

Histioneis is a rare genus; its delicacy, transparency, small size and limited investigations in warm/tropical waters in the last decades contribute to the scarce records. Little is known of its ecological and geographical distribution. Records of *Histioneis* from the north-western Pacific Ocean are restricted to a few citations along the coasts of Japan by Okamura (1912) and Abé (1967). Böhm (1936), Rampi (1952) and Balech (1962) reported several species from the tropical waters of the western and central Pacific Ocean. Wood (1963a,b) described several taxa from the surrounding waters of Australia. For the eastern Pacific Ocean, Kofoid and Skogsberg (1928), in the most complete study on *Histioneis* to date, described and well illustrated numerous species.

The present study describes and illustrates the abundance and composition, geographic and vertical distributions of *Histioneis* collected in several regions of the tropical and equatorial western Pacific Ocean.

Materials and methods

Samples were collected during 10 cruises in the western Pacific Ocean (Figure 1).

- Two cruises were carried out on board R/V *Soyo Maru* (13–20 May and 3–10 July 2002) along the meridian 138°E in the vicinity of the Kuroshio Current. Nine stations were sampled from 30°30′N to 34°15′N in May, and 10 stations from 30°0′N to 34°20′N during the July cruise. At each station, 15 depths from 5–200 m were sampled.
- R/V *Hakuho Maru* visited the Celebes, Sulu and South China Seas from 7 November to 18 December 2002. Samples were collected from 10 stations at six depths from 0–150 m.
- A cruise was carried out on board R/V *Mirai* (15–28 January 2003) along the equator from 160°E to 160°W. Samples were collected from 9 stations at 14 depths between 0–200 m. In addition, during the ship transit in returning to Japan, several 5-l samples were collected by pumping from ca. 5 m depth and filtering through 10-μm pore size Nylon mesh.
- Six cruises were completed at station H (41°30′N, 145°47′E) on board R/V *Oshoro Maru* and station A7 (41°30′N, 145°30′E) on board R/V *Wakataka Maru* in the Oyashio area during the spring and summer of 2003.

Samples collected by Niskin bottles were preserved with acidified Lugol's solution and stored at 5°C. Samples of 400 ml were concentrated via sedimentation in glass cylinders. Over five days, the top 350 ml of each sample was progressively and slowly siphoned off with small-bore tubing. Fifty ml of concentrate from 400 ml of water were settled in composite settling chambers. The entire chamber was scanned at 200× with an inverted Nikon (Tokyo, Japan) microscope equipped with a Nikon digital camera and the specimens of *Histioneis* were photographed for further precise identification. Film photographs were taken during a short period when the digital camera was unavailable.

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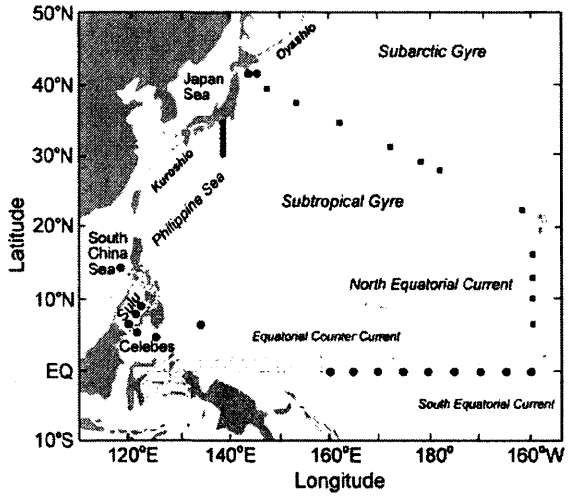


Figure 1 Map of the station locations marked by black circles in the western Pacific Ocean.
The black squares represent surface net sampling.

Results

A total of 65 specimens of *Histioneis* was recorded in the western Pacific Ocean and were tentatively assigned to 17 species (Figures 2–33). All specimens were observed as single cells, never in couplets of dividing cells, triads or tetrads (as occurs in other dinophyceans). *Histioneis cymbalaria* Stein *sec* Balech (1988), with a sulcal list tapering posteriorly to a point, or rounder and with a variable degree of reticulation, was the most common species (Figures 3–4, 9–13). One specimen with a less complexly ribbed sulcal list was tentatively assigned to *H. cleaveri* Rampi, being the first record after the original description (Figure 2). Specimens with a sulcal list with several radiating ribs from the main posterior rib and the posterior sulcal list more dorsally extended that *H. cymbalaria* were tentatively considered as *H. pacifica* Kofoid *et* Skogsberg (Figures 5–7). Figure 8 illustrates a tentatively immature specimen of a species related to the previous taxa. After *H. cymbalaria*, the most abundant species was *H. longicollis* Kofoid, and this species is assumed to show a variable development of the sulcal list (Figures 19–24). Several specimens, with less elongate appearance and shorter sulcal list lacking ornamentation in the posterior rib compared to *H. longicollis*, were considered to be *H. joergensenii* Schiller (Figures 17–18).

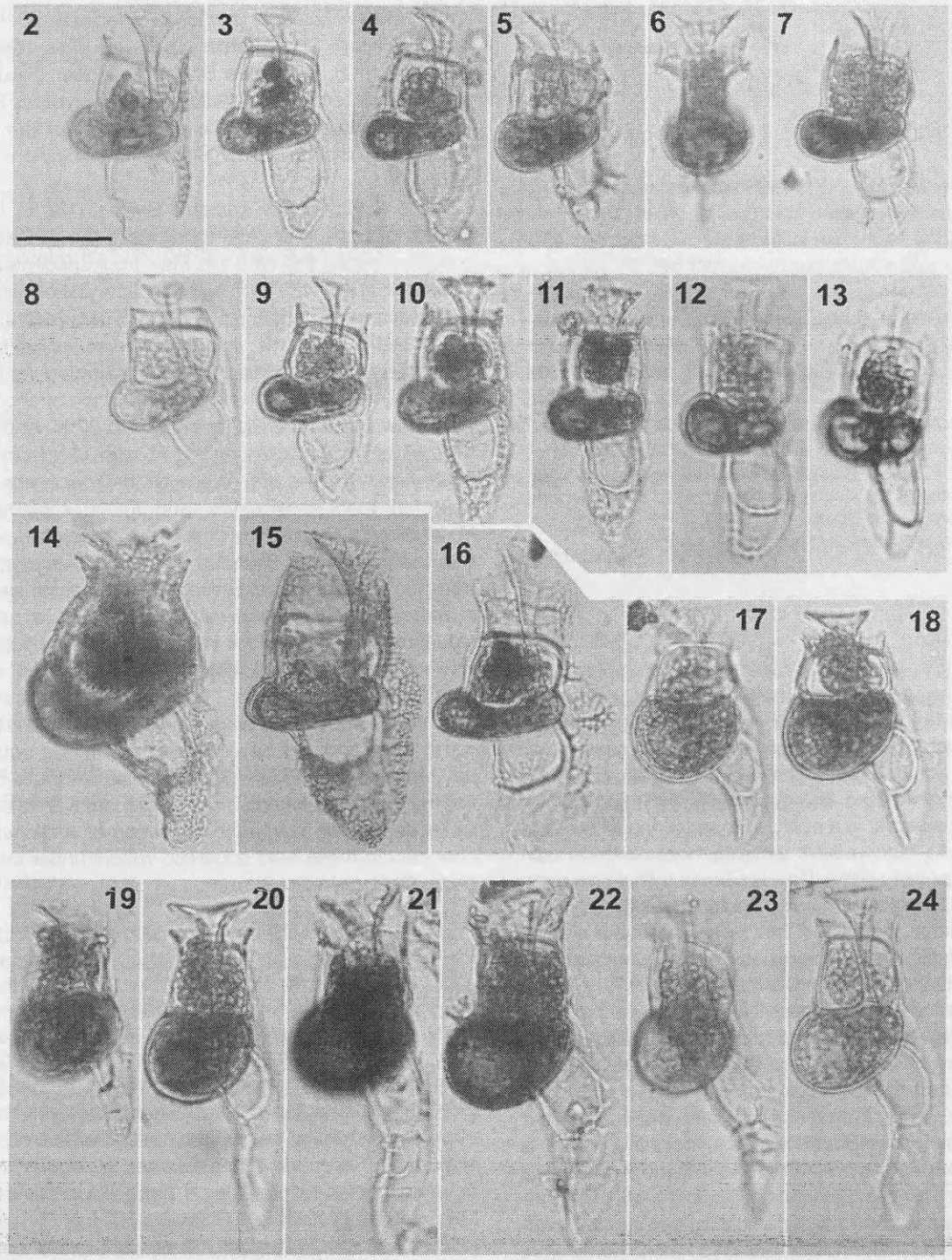
Other species were observed from single or a few specimens, such as *Histioneis pietschmannii* Böhm *in* Schiller from the South China Sea, *H. mitchellana* Murray *et* Whitting and *H. schilleri* Böhm *in* Schiller from the Philippine Sea (Figures 14–16). Two specimens were identified as *H. elongata* Kofoid *et* Michener (Figures 25–26) and another corresponded to *H. costata* Kofoid *et* Michener (Figure 27). One specimen from the Philippine Sea was tentatively assigned to *H. sphaeroidea* Rampi (Figure 29), being the first record beyond the Mediterranean Sea (Gómez 2003). The identification of several specimens of the former genus *Parahistioneis* were more difficult, e.g., *H. para* Murray *et* Whitting or *H. paraformis* (Kofoid *et* Skogsberg) Balech. The specimen in Figure 30 was assigned to *H. para*, and a larger specimen to *H. paraformis* (Figure 31). Another specimen was tentatively assigned to *H. pachypus* Böhm *in* Schiller (Figure 28), and another tentatively identified as *H. oxypteris* Schiller (Figure 32). In one case, the poor quality of the photomicrograph did not allow precise identification (Figure 33).

In the vicinity of the Kuroshio Current (138°E) 10 individuals of *Histioneis* were found from the 131 samples analysed during the cruise in May. Four specimens were collected at 32°N. The maximum abundance was only two specimens per sample (5 cells l^{-1}) (Figure 34). During the cruise in July, the stations were re-visited and 38 specimens were observed from 144 samples. As in May, the higher abundance was recorded in the offshore subtropical waters of the Philippine Sea at 32°N. At this station, 17 individuals were collected, with 13 specimens at 30 m depth (Figure 35). Nearly all the specimens corresponded to *H. cymbalaria*, and a few specimens to *H. longicollis*. During the cruise in the marginal seas of the western Pacific Ocean 9 specimens were recorded from the 81 samples examined. All the specimens were collected in the 0–30 m depth range, except for one individual at 150 m depth in the Sulu Sea (Figure 36). In the western and central equatorial Pacific Ocean, only 8 specimens were observed from the 124 samples analysed. All the specimens were found in the western Pacific warm pool and we have no records in the equatorial upwelling region (Figure 37). Samples from six cruises carried out off Hokkaido (north of Japan) were also analysed during this study. No specimen of *Histioneis* was observed in these cold subarctic waters under the influence of the Oyashio Current.

Discussion

Two species, *Histioneis cymbalaria* and *H. longicollis*, were the most common in the regions of the Pacific Ocean examined. However, previous studies in the area did not report these taxa. In the coastal waters off southern Japan, Okamura (1912) reported *H. highleyi* Murray *et* Whitting, *H. paraformis* (as *H. para*), *H. paulsenii* Kofoid (?*H. carinata* Kofoid or ?*H. elongata*) and *H. reticulata* Kofoid. Abé (1967) reported *H. hippoperoides* Kofoid *et* Michener, *H. pietschmanii* and *H. mitchellana*. These authors collected their samples from surface hauls in coastal waters. Net sampling facilitates collection of rare species of phytoplankton, but the smaller and fragile specimens may be inefficiently retained, and their abundances subsequently underestimated in comparison with larger or resistant congeneric taxa. In the present study, small species such as *H. cymbalaria* (<70 μm length) were more common in offshore oligotrophic waters (Figures 34–37). Iriarte and Fryxell (1995) only reported *H. longicollis* and *H.* cf. *mitchellana* in the central equatorial Pacific Ocean.

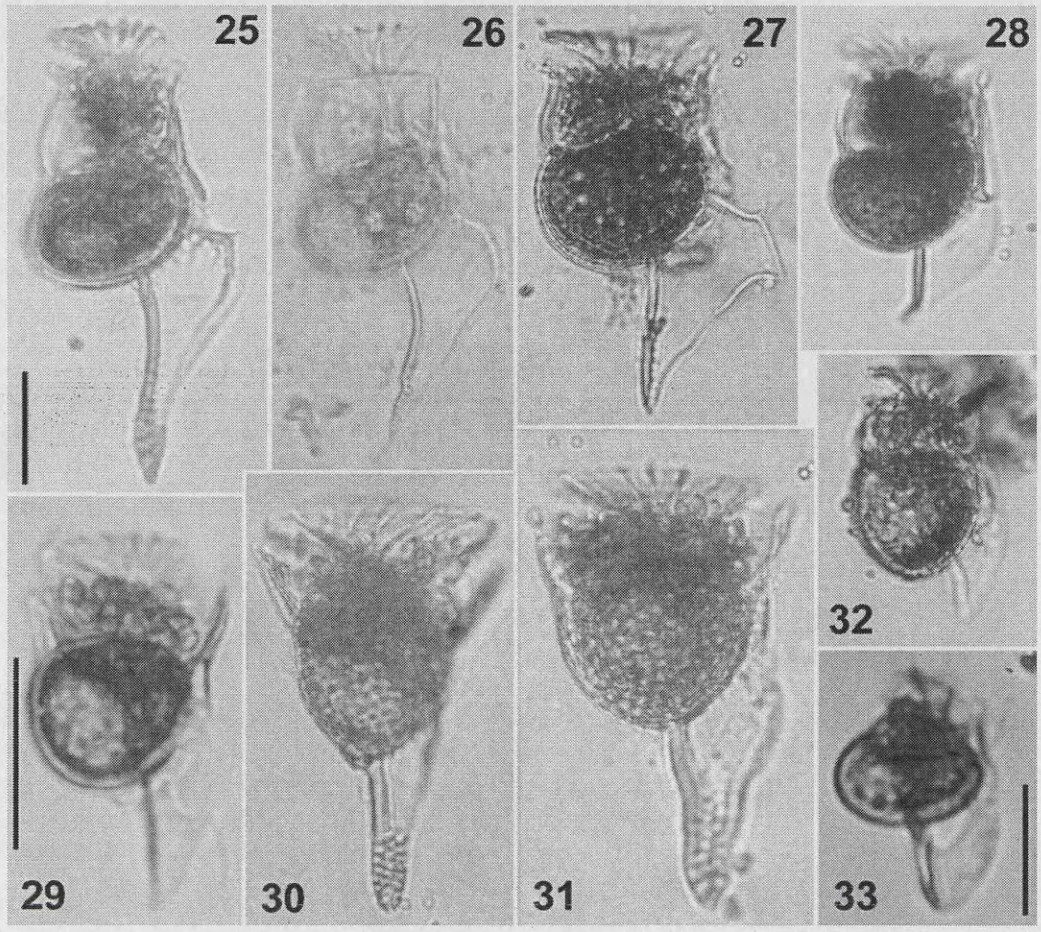
In general, *Histioneis* is a rare genus. Exceptionally, 13 specimens were found in one sample (32 cells l^{-1}). The hydrological and trophic conditions (major nutrients), and



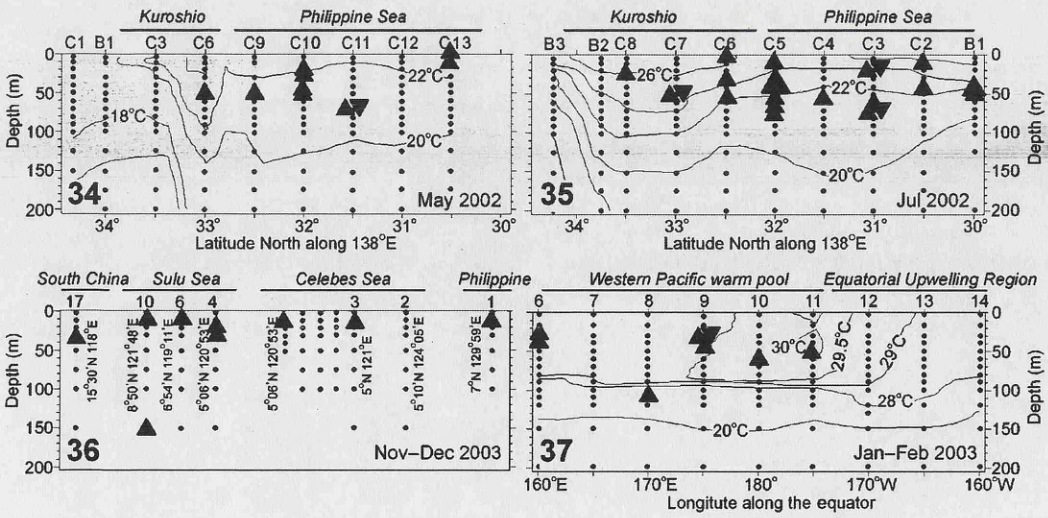
Figures 2–24 Photomicrographs, bright field optics, of *Histioneis* in right lateral view (except Figure 6 in dorsal view). (2) Tentatively *H. cleaveri* (33°N, 138°E; 50 m depth). (3–4, 9–13) Several specimens of *H. cymbalaria* sec Balech (1988). (5–6) Tentatively *H. pacifica* (0°, 175°W; 50 m depth). (7) Tentatively *H. pacifica* (0°, 180°; 60 m depth). (8) Unidentified specimen (0°, 180°; 0 m depth). (14) *H. pietschmannii* (14°30′N, 118°E; 30 m depth). (15) *H. mitchellana* (32°30′N, 138°E; 50 m depth). (16) *H. schilleri* (7°N, 130°E; 30 m depth). (17–18) *H. joergensenii*. (19–24) *H. longicollis*. All at the same magnification, scale bar=20 μm.

the phytoplankton assemblage at the collection site were investigated, and compared to the surrounding stations. Not one of these factors can be inferred as responsible for the higher abundance of *Histioneis* at this location. Along the equator, *Histioneis* was found from 170°E to 175°W, coinciding with high seawater temperatures (>29.5°C) and very oligotrophic conditions during El Niño in January 2003 (Figure 37).

The distribution of *Histioneis* was different from the autotrophic or mixotrophic species of *Dinophysis* that can achieve high abundance in eutrophic coastal waters. The apochlorotic *Histioneis* differs from *Dinophysis* in having a large cingular chamber that seems to be an adaptation for hosting unicellular cyanobacteria. These symbionts, named phaeosomes in early literature, were observed extracellularly in *Ornithocercus* and *Citharistes*



Figures 25–33 Photomicrographs, bright field optics, of *Histioneis* in right lateral view.
(25) *H. elongata* (32°N, 138°E; 50 m depth). (26) *H. elongata* (0°, 180°; 0 m depth). (27) *H. costata* (5°N, 121°E; 10 m depth). (28) Tentatively *H. pachypus* (7°N, 130°E; 10 m depth). (29) Tentatively *H. sphaeroidea* (33°30′N, 138°E; 20 m depth). (30) *H. para* (8°50′N, 121°48′E; 150 m depth). (31) *H. paraformis* (32°30′N, 138°E; 30 m depth). (32) Tentatively *H. oxypteris* (8°50′N, 121°48′E; 150 m depth). (33) Unidentified specimen (30°30′N, 138°E; 50 m depth). All at the same magnification, except Figure 29 and Figure 33; scale bars=20 μm.



Figures 34–37 Section plots of the records of *Histioneis* in the western Pacific Ocean indicated by black triangles (see Figure 1). (34) Records along the meridian 138°E in May. (35) Records from the same location in July. (36) Records from Celebes, Sulu and South China Seas. (37) Records from the western and central equatorial Pacific Ocean. The distribution of temperature is shown.

Stein and intracellularly in *Amphisolenia* Stein (Hallegraeff and Jeffrey 1984, Lessard and Swift 1986). In the present study, nearly all the specimens of *Histioneis* contained symbionts. The few exceptions were probably due to losses through sample treatment or damage to the cingular chamber. Norris (1967) described the rod-shaped, purple/pink cyanobacterium in *Histioneis* as *Synechococcus carcerarius* R.E. Norris. From living material, Lucas (1991) reported the presence of dividing cells in all the populations of symbionts, indicating active growth. He suggested that transmission of the symbiont in *Histioneis* occurs (rather that renewed infection). In the study of Hallegraeff and Lucas (1988), the food contents in *Histioneis* were not recognizable, but resembled cyanobacteria.

During the present study, samples were collected from the surface to 200 m depth. Nearly all the specimens were found in the upper 70 m depth (rarely just in the surface waters) and the highest abundance of *Histioneis* was at 30 m depth (Figures 34–37). If it is assumed that the cingular chamber functions as a greenhouse in which *Histioneis* grows symbionts to supplement its diet, the vertical position of *Histioneis* could be related to the optimal irradiance for the growth of these cyanobacteria. In the upper waters (<70 m depth) of the tropical Pacific Ocean, free-living unicellular cyanobacteria such as *Synechococcus* Nägeli are a ubiquitous component of the picoplankton with abundances of $\sim 10 \times 10^6$ cells l^{-1} (Blanchot et al. 2001). The vertical distribution of *Histioneis* could be related to the depth of maximal availability of potential prey and/or the optimal depth (irradiance) for the growth of the symbiont algae.

Histioneis has been reported rarely in the literature of the last three decades, mainly due to the limited taxonomical studies carried out in open waters of tropical oceans. Records at the species level are necessary to investigate the distribution and ecology of this genus.

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Synonymy and biogeography of the dinoflagellate genus *Histioneis* (Dinophysiales, Dinophyceae)

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Abstract: the genus *Histioneis* (=*Parahistioneis*) contains an excessive number of poorly described species, often based on the observation of a single specimen and ignoring the intraspecific variability. In order to investigate the validity of the species and to suggest synonyms, the original illustrations of all known species of *Histioneis* are reproduced and grouped based on the morphological similarity. The scarce records and the uncertainties on the identification at the species level are responsible of the lack of biogeographical information. Large and highly ornamented species tended to appear in tropical waters, whereas smaller and less ornamented species showed a wider distribution and they can also found in temperate waters such as the Mediterranean Sea.

Key words: *Histioneis*, *Parahistioneis*, Dinophysiales, dinoflagellate, phytoplankton, biogeography.

Histioneis Stein is a dinophysoid heterotrophic dinoflagellate especially adapted to highly stratified, sub-tropical and tropical oceanic waters. The cingular or phaeosome chamber was modified to harbor unicellular diazotrophic cyanobacteria and the orientation of the prominent left sulcal list was speculated to enhance a "feeding current" towards the sulcal region (Taylor 1980).
Kofoid and Skogsberg (1928) elegantly described numerous species in the most complete study on *Histioneis* to date. Schiller (1933) described several new species and illustrated all the species known at that time. Further species were described by Forti (1932), Böhm (1933, 1936), Rampi (1950, 1952, see references in Rampi and Bernhard 1980), Osorio-Tafall (1942), Gaarder (1954), Halim (1960) and Wood (1963a,b). Recently, Polat and Koray (2002) and Gómez (2005b) reported micrographs of species from the Mediterranean Sea and the Pacific Ocean, respectively.
Histioneis has a transverse or cross rib in the lower cingular list that is lacking in the genera *Parahistioneis* Kofoid & Skogsberg and *Ornithocercus* Stein. According to Wood (1968) more than six radial ribs in the posterior cingular list corresponded to *Ornithocercus* and less than six radial ribs to *Parahistioneis*. The species *Histioneis francescae* Murray & Whitting was transferred to *Ornithocercus* (Balech 1962). The genera *Histioneis* and *Parahistioneis* have been considered as synonyms because the cross rib is often hardly visible or it can be considered as a poor taxonomical characteristic for the generic separation (Balech 1988). Balech (1971) transferred *Parahistioneis*

paraformis whereas *P. acuta, P. acutiformis, P. conica, P. gascoynensis, P. pachypus, P. pieltainii, P. sphaeroidea* and *P. varians* have not been formally transferred to *Histioneis*. Further studies may split the genus *Histioneis* into several new genera with the re-establishment of *Parahistioneis*. Consequently at the present, the erection of new combinations, 35 years after the last one, would create more confusion.

More than 100 species have been described since the earliest description of the type species (*H. remora* Stein 1883) to the latest one (Rampi 1969), being one of the most numerous genus of marine dinoflagellates (Gómez 2005a). Nearly all the species were described from a single or few specimens and often with no further records after the initial description. Abé (1967), Balech (1971, 1988) and Taylor (1976) discussed on the validity of several species. The literature was often ancient and scattered, and no revision on the entire genus is available since Kofoid and Skogsberg (1928) and Schiller (1933). The identification at the species level is difficult due to the deficient delimitation of the species and it is uncertain how many species are valid. Within this context, little is known on the biogeography of *Histioneis*. The present study revises the synonymy of *Histioneis* in order to facilitate the identification at the species level and discusses on the geographical distribution.

MATERIALS AND METHODS

The original illustrations of all known species of *Histioneis* were reproduced and grouped based on the morphological similarity. Key diagnostic characters for the identification of the species include the cell body shape, primary ribs of the left sulcal list and the cingular list features (lateral pouch development, inclination of the upper cingular list). Other features such as the areolation of the hypotheca wall are characteristic of only a few taxa (i.e. *H. biremis*). For the descriptive terminology is important (Fig. 1): R_2 (middle rib) the fission rib, at the place where the list is divided by binary fission and R_3 (posterior main rib), the list near the posterior end of this list, if more than one rib is present in this region, the best developed of these (Kofoid and Skogsberg 1928). In species such as *H. longicollis*, a loop formed by the R_2 bending posteriorly and anastomosing with R_3 is here named "window". Several species also showed supplementary ribs (i.e. *H. megalocopa*).

RESULTS AND DISCUSSION

Several factors should take into account on the study of the validity of the species based on the original descriptions. Biological factors such as the unknown life cycle and its phenotypic

intraspecific variability, different degree of development after the division or morphological modifications as an adaptation to environmental turbulence conditions may be responsible of the description of morphotypes as separate species. In addition, the transparency of the hyaline structures may be responsible of incomplete descriptions and even new species may be described from specimens damaged through sample treatment.

The scarce records of *Histioneis* make difficult to assess the intraspecific variability. No species of *Histioneis* has been cultured and the only existing information on the life cycle of the Dinophysiales came from a few toxic species of *Dinophysis* Ehrenberg that have been temporally cultured. *Dinophysis* exhibited a high morphological variability, complicated by the existence of intermediate forms and the occurrence of "small cells" that have been previously considered to be different species (e.g. Reguera and González Gil 2001). The possible phenotypic variability was not considered in the description of the species of *Histioneis*, often based on single specimens. The size and shape of the sulcal list of *Histioneis* could vary as an adaptation to the turbulence conditions as reported for winged dinoflagellates such as *Ceratocorys horrida* Stein (Zirbel *et al.* 2000). Immature individuals of *Histioneis* could be described as new species. The degree of reticulation in the sulcal list probably depends on the maturation following the last division. As reported for *Dinophysis* the reticulation in the sulcal list was more pronounced on the fully developed-mature specimen and absent in the regenerated half of the list after division (e.g. Reguera and González Gil 2001). This factor may be especially relevant in species with supplementary ribs such as *H. megalocopa*. Different morphology of the sulcal list can be related to the phenotypic variability, whereas the variation in shape of the hypotheca is expected to be more conservative.

In addition to the incidence of natural factors, the delicate *Histioneis*, usually collected by net hauls, can be damaged through sample treatment. Incomplete individuals may be described as new species (i.e. *H. elegans* resembled a damaged individual of *H. villafranca*). The transparency of the hyaline fins of *Histioneis* can easily be overlooked being responsible of the incomplete descriptions (i.e. *H. elongata*). The line drawings of the original descriptions of some species have been excessively simplified as in Böhm (1933, 1936) and Wood (1963a,b) (i.e. *H. simplex*) and other illustrations seem to be over-stylized (i.e. *H. josephinae*). The cell size as a criterion for the species identification should be considered with caution due to the imprecise size measurements of the early descriptions. For example Stein (1883) did not provide information on the magnification of his figures, being misinterpreted by further authors. All these factors, especially the unknown morphological variability in the life cycle, could have been responsible for the excessive proliferation of new species of *Histioneis*.

Delimitation of groups and synonymy: The original descriptions and some illustrations by other authors were grouped based on morphological similarities. In the present study with no phylogenetic purposes and to facilitate the comparisons, the groups of species of *Histioneis* were mainly delimited by 1) the shape of the cell body (rotund, reniform, etc) and 2) the orientation and shape of the left sulcal list.

***Histioneis cymbalaria*-group:** (Figs 2-26) Confusion in the identification of the species of *Histioneis* began since the first publication. Stein (1883) described the type species, *H. remora*, and *H. biremis*, *H. crateriformis*, *H. megalocopa* and *H. cymbalaria*. For this last taxon, he reported three different lateral figures and one ventral view (Figs 3, 6, 12). Later, Schiller (1933) described *H. skogsbergii* based on one of the lateral views and the ventral view illustrated by Stein for *H. cymbalaria* (Fig. 3). Kofoid and Skogsberg (1928) considered other of the Schiller's figures of *H. cymbalaria* as a synonym of *H. hyalina* (Figs 6, 9). Two further described species, *H. depressa* and *H. schilleri* (Figs 7, 24), also resembled *H. cymbalaria*. From the observation of a single specimen, Taylor (1976) reported that *H. depressa* in many respects resembled a very small *H. mitchellana* in which the reticulation was reduced in complexity (Fig. 5). From abundant material, Balech (1988, p. 237) illustrated 3 morphotypes of *H. cymbalaria* (Figs 13-15). Balech considered *H. depressa* as a synonym of *H. cymbalaria*. *Histioneis depressa* has been illustrated with different morphology even by the same author (Fig. 4) (Wood 1963, 1968). One of the line drawings by Balech (1988) of *H. cymbalaria* was similar to Taylor's (1976) figure of *H. depressa* (Figs 5, 14). None of the illustrations by Taylor or Balech corresponded to Schiller's figure of *H. depressa* (Fig. 7). Gómez (2005b) observed several specimens of *H. cymbalaria* from the same sample that allowed the observation of the intraspecific variability. The tapering of the sulcal list of different specimens was pointed or rounded with variable perforation and the size (~60 µm length) was similar to that for *H. cymbalaria* sec Balech (1988) or *H. depressa* sec Taylor (1976). Stein (1883) did not provided information on the size of *H. cymbalaria*, but Schiller (1933) with no new observations of *H. cymbalaria* reported that the length was 130-160 µm. Balech (1988, p. 66) considered that the species described by Stein (1883) should be reduced in size to match with the real dimensions. The Schiller's compilation was commonly referenced for the identification for many authors working in the Mediterranean Sea. Consequently the Mediterranean specimens of *H. cymbalaria* that really measured 60-65 µm long, instead of 130-160 µm, may be assigned to species of similar morphology and smaller size such as *H. depressa*. *Histioneis depressa*, described from the cold waters of the northern Adriatic Sea, was one of the more commonly cited species in the Mediterranean whereas no record of *H. cymbalaria* existed (Gómez 2003). Beyond the possible *H. cymbalaria-depressa* synonymy, *H. cymbalaria* may be present in the Mediterranean Sea because

H. speciosa (Fig. 11), only known from the original description in the Mediterranean Sea, is here considered as synonym of *H. cymbalaria*. *Histioneis depressa* sec Polat and Koray (2002) showed a rounder cell body, the sulcal list was more ventrally deflected and had a lateral pouch compared to the original description. Further research should address whether *Histioneis depressa* and *H. cymbalaria* are conspecific or both co-occur in the Mediterranean Sea. Records beyond the Mediterranean Sea such as *H. depressa* sec Taylor (1976) corresponded to *H. cymbalaria* (Table 1). In addition to the confusion between *H. cymbalaria* and *H. depressa*, the species *H. hyalina* is considered a synonym of other of the Stein's figures of *H. cymbalaria* (Kofoid and Skogsberg 1928). Stein (1883) could try to show the intraspecific morphological variability of *H. cymbalaria* with three different illustrations. Stein's figure showed a specimen with a kidney-shaped cell body, whereas *H. hyalina* showed a rounder cell body and the sulcal list was more ventrally deflected (Figs 6, 9). Balech (1988, p. 66) already reported that the figures of *H. hyalina* by Kofoid and Skogsberg and by Stein corresponded to separate species. The illustration of *H. hyalina* by Wood (1963) was closer to *H. depressa* (Figs 4, 7).

Recently *Histioneis cleaveri* (Fig. 16) has been tentatively identified from the Pacific Ocean (Gómez 2005b). *Histioneis detonii*, only reported by Rampi from the Mediterranean and Pacific waters, showed a sulcal list that resembled members of the *cymbalaria*-group, but it differed in having a narrow reniform cell body (Fig. 25). *Histioneis rampii*, only know by the authority, showed a gibbous ventral margin and the cingular lists inclined (Fig. 17). *Histioneis robusta* is characterized by a margin extended ventrally (Fig. 18). *Histioneis skogsbergii*, described by Schiller based on one of Stein's figures of *H. cymbalaria* (Fig. 3), with the sulcal list tapering posteriorly to a point and highly reticulated, is considered here as a morphotype of *H. cymbalaria*. *Histioneis schilleri* (Fig. 24), larger than *H. cymbalaria* and characterized by a posterior list gibbous and reticulate margin, was a distinctive taxon often reported in the western Pacific Ocean (Table 1). Gómez (2005b) illustrated *H. schilleri* and *H. mitchellana*. *Histioneis schilleri* should not be considered a synonym of *H. mitchellana* contrary to the opinion by Taylor (1976). In the Caribbean Sea, Paulmier (2004) reported *H. cymbalaria*, but his figure corresponded to *H. schilleri*, which has been cited in that location (Díaz-Ramos 2000) (Table 1). *Histioneis bougainvillae* (Fig. 2), only known by the authority, showed a round cell body and several loops in the sulcal list that differed from other members of the *cymbalaria*-group. *Histioneis caminus*, with a very sketchy description, would require further research (Fig. 26).

A subgroup of species included in the *cymbalaria*-group is characterized by a saddle-shaped cell body that was higher dorsally. *Histioneis pietschmanii* was a distinctive taxon commonly reported in the Pacific Ocean (Gómez 2005b, Table 1). *Histioneis panaria* and *H. panda* differed in the size of the cingular list (Figs 19, 20). Norris (1969) reported that the hyaline fins of *H. panaria* could

easily go unnoticed. Abé (1967) proposed *H. pulchra* as a synonym of *H. mitchellana* (Figs 22, 23). Abé considered that the figures of *H. mitchellana* by Kofoid and Skogsberg (1928) also illustrated *H. pulchra*. Both taxa are here considered as separate species until further research.

***Histioneis longicollis*-group:** (Figs 27-46) The *longicollis*-group is characterized by a round cell body and the sulcal list inclined ventrally compared to the *cymbalaria*-group. In the *cymbalaria*-group the hypotheca was kidney or saddle-shaped and the sulcal list was more dorsally deflected. Both groups had a window formed by the R_2 bending posteriorly and anastomosing with R_3, quadrangular in members of the *cymbalaria*-group and circular in the *longicollis*-group (quasi triangular for *H. joergensenii*). *Histioneis longicollis* showed a high degree of variability in the development of the sulcal list, including specimens with a short sulcal list (Gómez 2005b). Schiller (1933) did not reproduce the original Kofoid's figure of *H. longicollis* (Figs 39, 40) and his figure resembled *H. hyalina* (Fig. 9). Halim (1960) reported *H. longicollis* from the Ligurian Sea and he described four close taxa: *H. elegans*, *H. faouzii*, *H. sublongicollis* and *H. villafranca* (Figs 27-31). The length of these taxa, 72 µm, agreed with *H. longicollis* sec Halim (Fig. 29). The four species, described from single or few specimens, mainly differed in the distal branches of the sulcal list. These taxa, only known by the authority (except *H. faouzii*, Rampi 1969), are here considered synonyms of *H. longicollis*. *Histioneis minuscula* (Fig. 32) was akin to specimens of *H. longicollis* with a scarcely developed sulcal list and together with *H. kofoidii* (Fig. 33) may be considered synonyms of *H. longicollis*.

Histioneis pacifica is characterized by the sulcal list inclined dorsally and several ribs radiated marginally from the window (Fig. 44). The sulcal list of *H. longicollis* was acuter and the cell body was rounder than in *H. pacifica*. Schiller (1933) suggested that *H. pacifica* and *H. hyalina* may be synonyms. *Histioneis pavillardii* differed from *H. bernhardii* in the more elongate appearance (Figs 43, 45). Both taxa were tentatively considered as synonyms of *H. pacifica*. *Histioneis imbricata* (Fig. 46), never reported after the initial description (Table 1), appeared to occupy an intermediate position between *H. longicollis* and *H. pacifica*. In *H. marchesonii* (Fig. 42), illustrated by Polat and Koray (2002), lacked the window, but otherwise resembled the *longicollis*-group. *Histioneis aequatorialis* with a well-developed dorsal sail and supplementary ribs resembled members of the *megalocopa*-group. However, *H. aequatorialis* was tentatively included in this group due to its rounded cell body (Fig. 41). *Histioneis longicollis* and *H. joergensenii*, two of the most common species in the Mediterranean Sea (Gómez 2003), may be synonyms according to the illustrations by Rampi and Bernhard (1980) (Figs 37, 38). The shape of the window was rounded in *H. longicollis* and quasi triangular in *H. joergensenii*. *Histioneis joergensenii* appeared to be intermediate between *H. vouckii* and *H. planeta* (Figs 34-36). For *H. vouckii* the R_2 and R_3 joined acutely in the margin of

the posterior part of a shorter sulcal list. *Histioneis planeta* showed a larger sulcal list that resembled *H. longicollis*.

***Histioneis elongata*-group:** (Figs 47-56) This group is characterized by a long R_3, the cross-rib extended ventrally and a smooth triangular sail extended from R_2 to R_3. Böhm (1936) illustrated the intraspecific variability of the sulcal list of *H. elongata* (Figs 51, 55). *Histioneis costata* mainly differed from *H. elongata* in the shorter R_3 and it cannot be discarded that both taxa may be conspecific (Figs 55, 56). *Histioneis isselii* showed an ornamented sulcal list and in some way resembled the members of the *longicollis*-group (Fig. 50). *Histioneis subcarinata* resembled *H. elongata* sec Böhm (1936) (Figs 49, 51). *Histioneis carinata* differed from other members of this group in the narrow cell body (Fig. 48). *Histioneis elongata* var. *curvata* showed a less rotund cell body than *H. elongata*. Its cell body resembled *H. subcarinata* and the sulcal list of *H. elongata* var. *curvata* only differed from that taxon in the occurrence of the marginal sail that extended dorsally behind R_3 (Figs 47, 49). *Histioneis moresbyensis* differed mainly from *H. costata* in the R_2 bent sharply backwards and the more ellipsoidal cell body (Fig. 54). If the bent R_3 of *H. moresbyensis* with a dorsal supplementary rib is projected in the vertical axis of the cell, this taxon resembled *H. australiae* (Fig. 53). The cell body of *Histioneis lanceolata* (Fig. 52) was rotund and as in *H. australiae* showed a supplementary rib branching dorsally behind R_3. These last three species, never reported after the initial descriptions, need further research (Table 1).

***Histioneis para*-group:** (Figs 57-62) The species of this group are characterized by a long R_3, almost in the vertical axis of the cell and the cingular lists wide and ribbed. Most of the species of this group and several species of the next two groups have been described as *Parahistioneis*. The hypotheca was hemispherical for *H. paraformis* (Figs 59, 61) and more triangular for *H. para* (Fig. 58). The original description of *H. para* and that by Kofoid and Skogsberg (1928) showed slight differences in the sulcal list (Figs 59, 61). *Parahistioneis conica* is here considered as a synonym of *H. para* (Figs 57, 58) and *P. acuta* is tentatively considered as a synonym of *H. paraformis* (Figs 59-61). *Histioneis rotundata* is included in this group although it showed a slightly bent R_3 and the margin undulated (Fig. 62).

***Histioneis garrettii*-group:** (Figs 63-74) This group is characterized by a R_3 that extended straight almost in the vertical axis of the cell, but the R_3 was shorter than in the previous group. Several species had a supplementary rib from R_3 dorsally. *Histioneis karstenii* (Fig. 63) showed a relatively large epitheca, non-pedunculate anterior cingular list and an elongated margin that in some way resembled *Ornithocercus*. *Histioneis garrettii* sec Balech (1988) resembled *H. diomedeae* in the

body shape and ventral cross-rib (Figs 66, 67). *Histioneis garrettii* sec Balech (1988) showed the R_2 and R_3 more ventrally deflected than in the original description of *H. garrettii* and showed the anterior cingular list wider and the sail branching dorsally from R_3 less developed (Fig. 66). Schiller (1933) included *H. dentata* (Fig. 64) in the *biremis*-group. The species *P. pachypus* and *P. varians* are synonyms (the former has the priority) (Figs 68, 69). *Histioneis gregoryi* (Fig. 70) showed more elongate appearance than *P. pachypus*. *Parahistioneis sphaeroidea* and *P. pieltainii* showed a similar shape of the sulcal list, being more ornamented in *P. pieltainii* that also showed the upper cingular list inclined (Figs 72, 73). Gómez (2005b) illustrated a tentative *P. sphaeroidea* that, if valid, constituted the first observation after the initial description (Table 1). The original illustration of *H. tubifera* was very sketchy and only known by the authority (Fig. 71, Table 1). *Parahistioneis pieltainii*, *P. sphaeroidea* and *H. tubifera* may be synonyms. Hernández-Becerril *et al.* (2003) suggested the synonymy of *P. pieltainii* and *H. isselii*.

The type species, *H. remora*, with a long R_3 is included here only based on the general appearance (Fig. 74). According to Böhm (1936), *H. remora* illustrated by Jørgensen (1923) could correspond to *H. elongata*. The records of the type species have been scarce and often misidentified due to the insufficient description by Stein (1883).

***Histioneis crateriformis*-group:** (Figs 75-84) This group is closely related to the *garrettii*-group, but with a more ventrally deflected R_3. The hypotheca was semicircular and usually the cingulum broad. As in the previous group, there was a high number of closely related species and immature specimens may be described as new species. Species such as *H. paulsenii* and *H. reticulata* were described from single specimens (Figs 78, 83). *Histioneis reticulata* could correspond to specimens with a scarcely developed sulcal list of *H. crateriformis* (Fig. 80). Balech (1971) considered *H. reticulata* and *H. crateriformis* as synonyms and later as separate species (Balech 1988). The sulcal list of the Balech's figure of *H. reticulata* (Fig. 81) was closer to *H. crateriformis* (Fig. 80), whereas the Balech's figure of *H. crateriformis* (Fig. 82) was closer to *H. mediterranea* (Fig. 84) and *H. mediterranea* sec Rampi and Bernhard (1980) (Fig. 85). *Histioneis mediterranea* resembled *H. reticulata* (Figs 83, 84). Balech (1988, p. 63) observed abundant material of *H. crateriformis* and he considered that the original Stein's figure was incomplete. Paulmier (2004, p. 201) illustrated a specimen identified as *H.* cf. *crateriformis*. *Histioneis oxypteris* (Fig. 79), tentatively identified by Gómez (2005b), resembled *H. crateriformis* and *H. paulsenii*. According to Balech (1988), *H. paulsenii* in Norris (1969) included *H. reticulata* and *H. crateriformis*. *Histioneis crateriformis* sec Balech (1988) resembled *P. pachypus* (Fig. 68). The small size of the specimens and the short sulcal list made the delimitation of the species of this group especially difficult. Taken into account the high intraspecific variability reported for *Dinophysis*, *H. reticulata* is here considered as

synonym of *H. crateriformis* and also probably *H. mediterranea* and *P. pachypus*. *Parahistioneis gascoynensis* (Fig. 77) is only known by the authority (Table 1). *Parahistioneis acutiformis* was similar to *H. diamantinae* in the sulcal list, but the orientation of the R_3 was different (Figs 75, 76).

***Histioneis inclinata*-group:** (Figs 85-90) This group is characterized by a left sulcal list short, ending ventrally and with a round margin. *Histioneis mediterranea* according to Rampi and Bernhard (1980) resembled *H. dubia*, being the R_3 illustrated in the former taxon (Figs 85, 86). *Histioneis alata* differed from *H. inclinata* in the larger sulcal list, ending more ventrally in *H. inclinata*. Both taxa, with the R_3 absent, may be synonyms (Figs 87, 88). *Histioneis inornata* differed from other members in the large cingular chamber and a short bent R_3 (Fig. 89). The sketchy illustration of *H. simplex* could correspond to the shape of *H. alata,* but both taxa differed in the shape of the cell body (Fig. 90).

***Histioneis gubernans*-group:** (Figs 91-99) This group is characterized by a rotund cell body and the R_3 and R_2 deflected ventrally with round margins and forming loops. The four illustrations of *H. variabilis* reported by Schiller (1933) showed the intraspecific variability. *Histioneis steinii* Schiller (non *H. steinii* Lemmermann) is a nomenclatural synonym of *H. variabilis*. According to Balech (1988) *H. variabilis* was a synonym of *H. striata* (Figs 94, 95, illustrated by Polat and Koray 2002). *Histioneis parallela* (Fig. 93) is here also considered as a synonym of *H. striata. Histioneis cerasus* showed the R_2 and R_3 almost parallel and branched marginally (Fig. 92). As reported by Taylor (1976), *H. fragilis* seems to be an immature specimen lacking that part of the left sulcal list posterior to the R_2 (Fig. 91). Sournia (1986, p. 153) illustrated an unidentified *Histioneis* which sulcal list resembled that of *H. fragilis*, but it differed in having a saddle-shape cell body (Fig. 100). *Histioneis ligustica* and *H. expansa* may be considered conspecific based on the original illustrations (Figs 96, 97). Polat and Koray (2002) illustrated the latter taxon. Both taxa only showed slight differences in the outline and ornamentation of the sulcal list and they are here considered as synonyms of *H. gubernans* (Fig. 98). *Histioneis reginella*, with the accessory lists that characterized *megalocopa*-group, has been included here due to the rotund cell body (Fig. 99).

***Histioneis megalocopa*-group:** (Figs 100-106) This group differed from the previous one in having a reniform cell body. The sulcal list achieved the highest degree of development with accessory lists. These ornamented species were likely to suffer breakage of the accessory lists through sample treatment. There were not reasons to consider *Histioneis milneri*, *H. helenae* and *H. hippoperoides* as separate species (*H. milneri* has the priority) (Figs 101-103). *Histioneis megalocopa* and *H.*

dolon are here considered as synonyms contrary to Balech (1988) (Figs 104, 105). *Histioneis josephinae* (Fig. 106) may be an extremely elaborated form of *H. megalocopa*.

***Histioneis navicula*-group:** (Figs 107-108) This group is composed of *Histioneis navicula* and *H. oceanica* that were not ascribed to any of the previous groups (Figs 107, 108). Both taxa, never reported after the initial descriptions (Table 1), showed a very narrow cell body and a large cingular chamber. *Histioneis navicula* (Fig. 107) resembled *H. panda* (Fig. 19). The sulcal list of *H. oceanica* (Fig. 108) resembled *H. elongata* var. *curvata* (Fig. 47), but it differed in having a narrow subreniform cell body. These rare taxa may be conspecific (*H. navicula* has the priority).

***Histioneis biremis*-group:** (Figs 109-111) *Histioneis highleyi* and *H. biremis* showed a distinctive Y-shaped and sigmoid areolated hypotheca, respectively (Figs 109, 110). These species seem to be a transition between *Histioneis* and *Citharistes* Stein. Ojeda (1999) illustrated a specimen of *Histioneis* (Fig. 111) with a distinctive pear-shaped hypotheca and the sulcal list as in *H. elongata* sec Böhm (1936). The sharper extreme of the hypotheca of *H. biremis* was more posteriorly deflected than in Ojeda's specimen (Figs 110, 111).

Biogeography: The distribution of *Histioneis* is restricted to warm waters. The northern records in the NW Pacific appeared associated with the warm waters of the Kuroshio Current (Okamura 1912, Abé 1967). Wood (1964) reported that *Histioneis* did not occur below 17ºC in the southern waters of Australia. Balech (1988) exceptionally recorded one specimen of *H. cymbalaria* at 13ºC and other of *H. highleyi* at 10ºC in the South Atlantic Ocean.

In the open north-western Pacific Ocean, the most ubiquitous species were *Histioneis longicollis* and *H. cymbalaria* (Gómez 2005b). It should be taken into account that net sampling does not allow collecting the smaller and fragile specimens. Consequently historical studies based on net hauls could underestimate the occurrence of these taxa versus larger and resistant species.

Histioneis biremis and *H. highleyi* are easily identifiable and distinctive species. To the best of my knowledge, the distribution of *H. biremis* is restricted to the Indo-Pacific region with one ancient record in the tropical Atlantic Ocean (Murray and Whitting 1899) (Table 1). *Histioneis highleyi*, a common species in the coastal waters of the western Pacific Ocean (Böhm 1936), is also known from the Atlantic Ocean (Table 1). None of both taxa is known from the Mediterranean Sea.

Forty species of *Histioneis* have been cited in the Mediterranean Sea, being the type locality of 27 species. This substantial species richness can be attributed, in part, to the historical tradition of taxonomic studies. A total of 13 species are exclusively known from the Mediterranean Sea (Gómez 2006). However, the consideration as endemic species should be cautiously considered due to

doubts in the validity of these taxa. *Histioneis depressa* (=?*H. cymbalaria*), *H. joergensenii* and *H. longicollis* were the most common species, followed by *H. marchesonii*, *H. inclinata*, *H. mediterranea* and *H. variabilis* (Gómez 2003). It can be expected more records of *Histioneis* in the warmer sub-basins of the Mediterranean. However, most of the records of *Histioneis* are reported in the colder sub-basins such as Ligurian and Adriatic Seas (Gómez 2003) because the warmer areas such as the South Ionian Sea are nearly unexplored. Apparently in the Mediterranean Sea were lacking species of *Histioneis* with accessory ribs such as *H. megalocopa* and *H. milneri*. Other large distinctive ornamented taxa such as *H. mitchellana*, *H. pietschmannii* or *H. schilleri* are known from tropical waters such as the Caribbean Sea, but they are absent from temperate waters such as Mediterranean Sea.

Zirbel *et al.* (2000) concluded that *Ceratocorys horrida* increased the length of the extensions under low turbulence conditions as a strategy to reduce the sinking speed. The low turbulence conditions that prevail in stratified tropical waters may favor species of *Histioneis* with large sulcal lists. In addition, the size and shape of the left sulcal list may be an adaptation for the capture of preys by modulating a feeding current (Taylor 1980). Consequently a large sulcal list may reduce the sinking speed and facilitate the capture of picoplankton preys.

In addition to the highly developed sulcal list that characterizes *Histioneis*, all the species have developed an especial chamber to harbor unicellular diazotrophic cyanobacteria that may constitute a supplement of the diet for the dinoflagellate. The microalgal preys may be found in wide geographical range. However, the requirements of the diazotrophic cyanobacteria could limit the geographical distribution of *Histioneis*. The dinitrogen fixation tended to be favored at high temperatures and this may explain the warm-water distribution of *Histioneis*. In cold waters or environments with a high abundance of microalgal preys, the costs of carrying an empty large cingular chamber would render *Histioneis* less competitive versus other heterotrophic dinoflagellates.

When the specimens cannot be illustrated and in case of doubts in the identification, it is recommended that the records will be assigned to the closer species of *Histioneis* by using "cf." before the epithet instead of *Histioneis* sp. This would facilitate further studies on the biogeography of *Histioneis*.

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Resumen: El género *Histioneis* (=*Parahistioneis*) contiene un excesivo número de especies, insuficientemente descritas y a menudo a partir de la observación de un solo espécimen ignorando la variabilidad intra-específica. Con el objetivo de investigar la validez de las especies y sugerir sinónimos, las ilustraciones originales de *Histioneis* se han reproducido y agrupado según su parecido morfológico. Las escasas observaciones de *Histioneis* y las dudas en la identificación a nivel de especie son responsables de la falta de información sobre su distribución geográfica. Las especies de mayor tamaño y más ornamentadas son típicas de aguas tropicales, mientras que especies más pequeñas y menos ornamentadas presentan una distribución más amplia y pueden encontrarse también en aguas más templadas como el Mar Mediterráneo.

Palabras clave: *Histioneis*, *Parahistioneis*, Dinophysiales, dinoflagelado, fitoplancton, biogeografía.

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TABLE 1

List of species of Histioneis *and* Parahistioneis *and the geographical distribution.*

Taxa	Distribution
P. acutiformis Rampi 1947 (=?*H. diamantinae*)	M(13),P(35)
P. acuta Böhm 1931 *in* Schiller 1933 (=?*H. paraformis*)	A(19,25,49),I(39)
H. aequatorialis Wood 1963	Au(47)
**H. alata* Rampi 1947 (=*H. inclinata*)	M(13)
H. australiae Wood 1963 (=?*H. moresbyensis*)	Au(47)
**H. bernhardii* Rampi 1969 (=*H. pacifica*)	M(13)
H. biremis Stein 1883	A(28),I(43),P(2,19,31,37)
H. bougainvillae Wood 1963	Au(47)
H. caminus Böhm 1931 *in* Schiller 1933	I(39)
H. carinata Kofoid 1907	I(5),Au(46),P(23)
H. cerasus Böhm 1931 *in* Schiller 1933	M(13),A(49),I(5,48),Au(47)
H. cleaveri Rampi 1952	P(?14,37)
P. conica Böhm 1931 *in* Schiller 1933 (=*H. para*)	I(39),P(8)
H. costata Kofoid & Michener 1911 (=?*H. elongata*)	I(5,39,48),Au(47),P(5,14,23)
H. crateriformis Stein 1883 (=*H. reticulata*,=?*P. pachypus*)	A(3,4,12,19,26,28,33,41,49),I(15,40),Au(47)
H. cymbalaria Stein 1883 (=*H. skogsbergii*,=*H. speciosa*,=*H. depressa* sec Taylor 1976)	A(3,4,19,30,?33,41),I(?43),Au(46,47),P(14,35,37)
H. dentata Murray & Whitting 1899	A(28)
H. depressa Schiller 1928 (?=*H. cymbalaria*)	M(13,34),A(3,25,49),I(5,15,40,?43),Au(46,47)
H. detonii Rampi 1947 (=?*H. cleaveri*)	M(13),P(36)
H. diamantinae Wood 1963 (=?*P. acutiformis*)	Au(17,46,47)
H. dolon Murray & Whitting 1899 (=*H. megalocopa*)	A(4,22,28,29),I(5,39,40,43,48),Au(16,46,47),P(2,23)
H. dubia Böhm 1933 (=?*H. mediterranea* sec Rampi)	M(6)
**H. elegans* Halim 1960 (=*H. longicollis*)	M(13)
H. elongata Kofoid & Michener 1911 (=*H. subcarinata*,=?*H. costata*)	M(34),A(49),I(5,48),Au(47),P(5,14,23,37)
**H. elongata* var. *curvata* Wood 1963 (=?*H. carinata*)	Au(47)
H. expansa Rampi 1947 (=*H. gubernans*)	M(13,34)
**H. faouzii* Halim 1960 (=*H. longicollis*)	M(13)
**H. fragilis* Böhm 1931 *in* Schiller 1933 (? . *milneri*)	M 13 ,I(5
H. garrettii Kofoid 1907	A(4),Au(47),P(7,23)
P. gascoynensis Wood 1963	A(49),Au(47)
H. gregoryi Böhm 1936 (=?*P. pachypus*)	P(7)
H. gubernans Schütt 1895 (=*H. expansa*,=*H. ligustica*)	M(13),I(39),P(39)
H. helenae Murray & Whitting 1899 (=*H. milneri*)	A(12,28,49),I(48),Au(47),P(2,23,37)
H. highleyi Murray & Whitting 1899	A(3,4,22,28,30),I(43),Au(47),P(5,24,31)
H. hippoperoides Kofoid & Michener 1911 (=*H. milneri*)	M(13),A(4,19,25,26,29,49),I(5,15,43),Au(46),P(1,23)
H. hyalina Kofoid & Michener 1911	M(13),A(3,4,25,49),I(5,40,43,48),Au(47),P(23,45)
H. imbricata Halim 1960 (=?*H. longicollis*)	M(13)

H. inclinata Kofoid & Michener 1911 (=*H. alata*)	M(13),A(4,26,30,49),I(5,48),Au(47),P(23,37)
H. inornata Kofoid & Michener 1911	A(49),Au(47),P(23)
H. isselii Forti 1932 (=?*H. elongata* sec Böhm,=?*P. pieltainii*)	M(13),A(9),P(19)
H. joergensenii Schiller 1928 (=?*H. vouckii*,=?*H. planeta*)	M(13),A(19,26,49),Au(47), P(14)
H. josephinae Kofoid 1907	P(23)
H. karstenii Kofoid & Michener 1911	M(13),P(7,23,37)
H. kofoidii Forti & Issel 1925 (=*H. longicollis*)	M(13)
H. lanceolata Wood 1963	Au(47)
**H. ligustica* Rampi 1940 (=*H. gubernans*,=*H. expansa*)	M(13)
H. longicollis Kofoid 1907 (=*H. elegans, H. faouzii, H. kofoidii, H. minuscula, H. sublongicollis, H. villafranca*)	M(13),A(10,49),I(5,48),Au(47),P(5,7,14,20,23,45)
H. marchesonii Rampi 1941	M(13,34)
H. mediterranea Schiller 1928 (=?*H. reticulata*)	M(13),A(3)
H. megalocopa Stein 1883 (=*H. dolon*)	I(5), P(41)
H. milneri Murray & Whitting 1899 (=*H. helenae*,=*H. hippoperoides*)	A(4,12,28,30,49),I(5,48),Au(47),P(2,7,37)
**H. minuscula* Rampi 1950 (=*H. longicollis*)	P(36)
H. mitchellana Murray & Whitting 1899 (=?*H. pulchra*)	A(4,12,28,30),I(39,43),Au(16,17,47),P(1,14,19,20,23,39)
H. moresbyensis Wood 1963 (=?*H. costata*)	Au(47)
H. navicula Kofoid 1907 (=?*H. oceanica*)	P(23)
**H. oceanica* Rampi 1950 (=?*H. navicula*)	P(36)
H. oxypteris Schiller 1928 (=?*H. paulsenii*)	M(13),A(4,30,49),Au(47), P(?14,45)
P. pachypus Böhm 1931 *in* Schiller 1933 (=*P. varians*,=?*H. gregoryi*,=?*H. crateriformis* sec Balech 1988)	I(39),Au(16,47),P(5,14)
H. pacifica Kofoid & Skogsberg 1928 (=?*H. pavillardii*,=?*H. bernhardii*)	A(29),I(5),P(14,23)
H. panaria Kofoid & Skogsberg 1928 (=?*H. panda*)	A(29,49),I(48),Au(47),P(23)
H. panda Kofoid & Michener 1911 (=?*H. panaria*)	A(19,25,29,49),I(43),Au(47),P(23)
H. para Murray & Whitting 1899 (=*P. conica*)	M(34),A(4,19,25,28,30,49),I(43),Au(16,17),P(2,14,24)
H. paraformis (Kofoid & Skogsberg 1928) Balech 1971 (=?*H. acuta*)	M(13),A(25,29,49),I(5,40),Au(47),P(7,14,19,36,37)
**H. parallela* Gaarder 1954 (=*H. striata*)	A(12)
H. paulsenii Kofoid 1907 (=?*H. crateriformis*,=?*H. reticulata*)	A(29),I(5),Au(47),P(23)
H. pavillardii Rampi 1939 (=*H. pacifica*)	M(13),A(27)
P. pieltainii Osorio-Taf 1942 (=?*P. sphaeroidea* =?*H. tubi ra* =?*H. isselii*)	
H. pietschmannii Böhm 1931 *in* Schiller 1933	A(12,49),I(5),Au(47),P(1,2,14,36,37,38)
H. planeta Wood 1963 (=?*H. joergensenii*,=?*H. longicollis*)	Au(18,21,47)
H. pulchra Kofoid 1907 (=?*H. mitchellana*)	A(12,22,26,49),I(40,43),Au(17,47),P(23)
H. rampii Halim 1960 (=?*H. cymbalaria*)	M(13)
H. reginella Kofoid & Michener 1911	P(23)
H. remora Stein 1883 (=?*P. sphaeroidea*)	M(13),A(49),I(48),Au(47)
H. reticulata Kofoid 1907 (=*H. crateriformis*,=?*P. pachypus*)	A(4,30),I(5),Au(46),P(7,23,24,31,38,45)
H. robusta Rampi 1969	M(13),A(27)
. ***rotundata*** Kofoid & Michener 1911	A(4,19,22,25,26,30,49),I(5,42),Au(46,47),P(23)

H. schilleri Böhm 1931 *in* Schiller 1933	A(9),I(5),Au(47),P(5,7,14,24)
H. simplex Wood 1963	Au(47)
**H. skogsbergii* Schiller 1933 (=*H. cymbalaria*)	Unknown
**H. speciosa* Rampi 1969 (=*H. cymbalaria*)	M(13)
P. sphaeroidea Rampi 1947 (=?*P. pieltainii*,=?*H. tubifera*)	M(13), P(?14)
**H. steinii* Schiller 1928 (=*H. variabilis*)	M(39)
H. striata Kofoid & Michener 1911 (=*H. variabilis*,=*H. parallela*)	M(34),A(4,19,26,30),I(5),P(23,37)
H. subcarinata Rampi 1947 (=*H. elongata*)	M(13),A(3)
**H. sublongicollis* Halim 1960 (=*H. longicollis*)	M(13)
H. tubifera Böhm 1931 *in* Schiller 1933 (=?*P. pieltainii*,=?*P. sphaeroidea*)	A(49),I(5)
H. variabilis Schiller 1933 (=*H. striata*,=*H. steinii*)	M(13),A(25,29,49),I(48),Au(47)
**P. varians* Böhm 1933 (=*P. pachypus*)	M(13)
**H. villafranca* Halim 1960 (=*H. longicollis*)	M(13)
H. vouckii Schiller 1928 (=?*H. joergensenii*)	M(13),A(49),I(5,11),Au(44,47)

(*) Taxa only known by the authority; **Bolt** type for sufficiently known species; M=Mediterranean, A=Atlantic, I=Indian, Au=Australia, P=Pacific Ocean. References: **1** = Abé (1967), **2** = Balech (1962), **3** = Balech (1971), **4** = Balech (1988), **5** = Böhm (1931), **6** = Böhm (1933), **7** = Böhm (1936), **8** = Chen and Ni (1988), **9** = Díaz-Ramos (2000), **10** = Dodge (1993), **11** = Dorgham and Moftah (1986), **12** = Gaarder (1954), **13** = Gómez (2003). **14**. Gómez (2005b), **15** = Halim (1969), **16** = Hallegraeff (1988), **17** = Hallegraeff and Jeffrey (1984), **18** = Hallegraeff and Reid (1986), **19** = Hernández-Becerril *et al.* (2003), **20** = Iriarte and Fryxell (1995), **21** = Jeffrey and Hallegraeff (1987), **22** = Käsler (1938), **23** = Kofoid and Skogsberg (1928), **24** = Konovalova (2000), **25** = Lessard and Swift (1986), **26** = Licea *et al.* (2004), **27** = Moita and Vilarinho (1999), **28** = Murray and Whitting (1899), **29** = Norris (1969), **30** = Ojeda (1999), **31** = Okamura (1912), **32** = Osorio-Tafall (1942), **33** = Paulmier (2004), **34** = Polat and Koray (2002), **35** = Rampi (1948), **36** = Rampi (1950), **37** = Rampi (1952), **38** = Ricard (1970), **39** = Schiller (1933), **40** = Sournia (1970), **41** = Stein (1883), **42** = Subrahmanyan (1958), **43** = Taylor (1976), **44** = Tong *et al.* (1998), **45** = Venrick (1982), **46** = Wood (1954), **47** = Wood (1963a,b), **48** = Wood (1963c), **49** = Wood (1968).

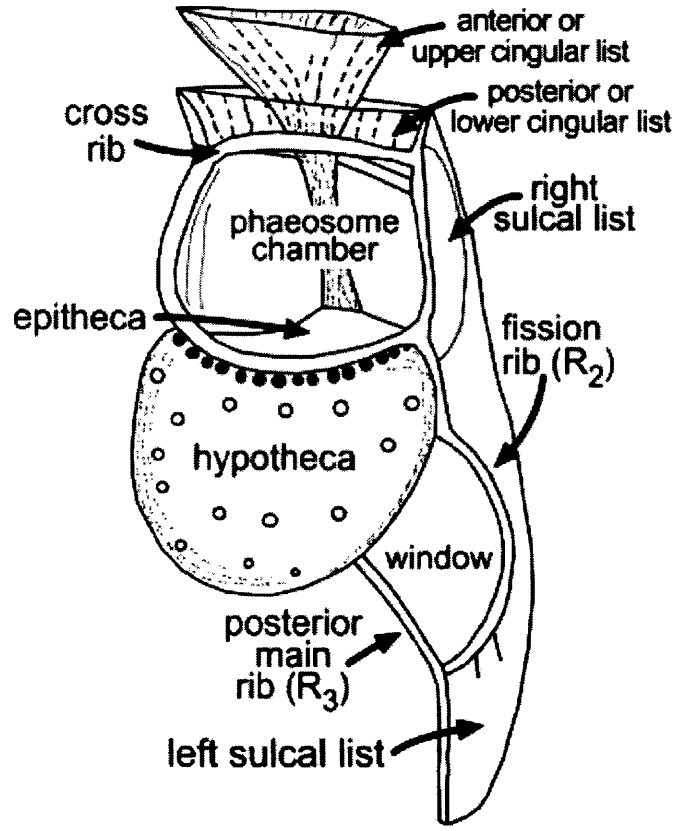
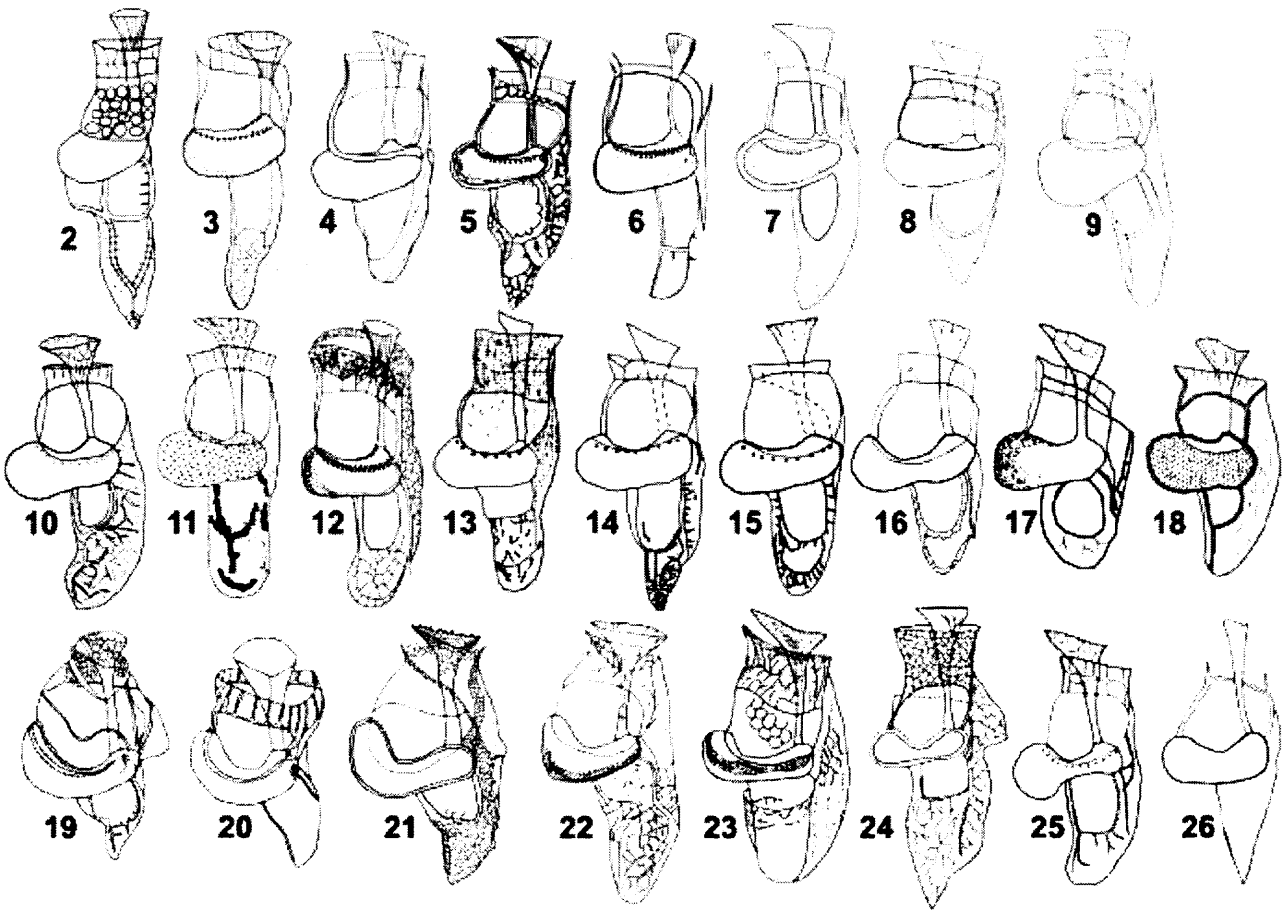
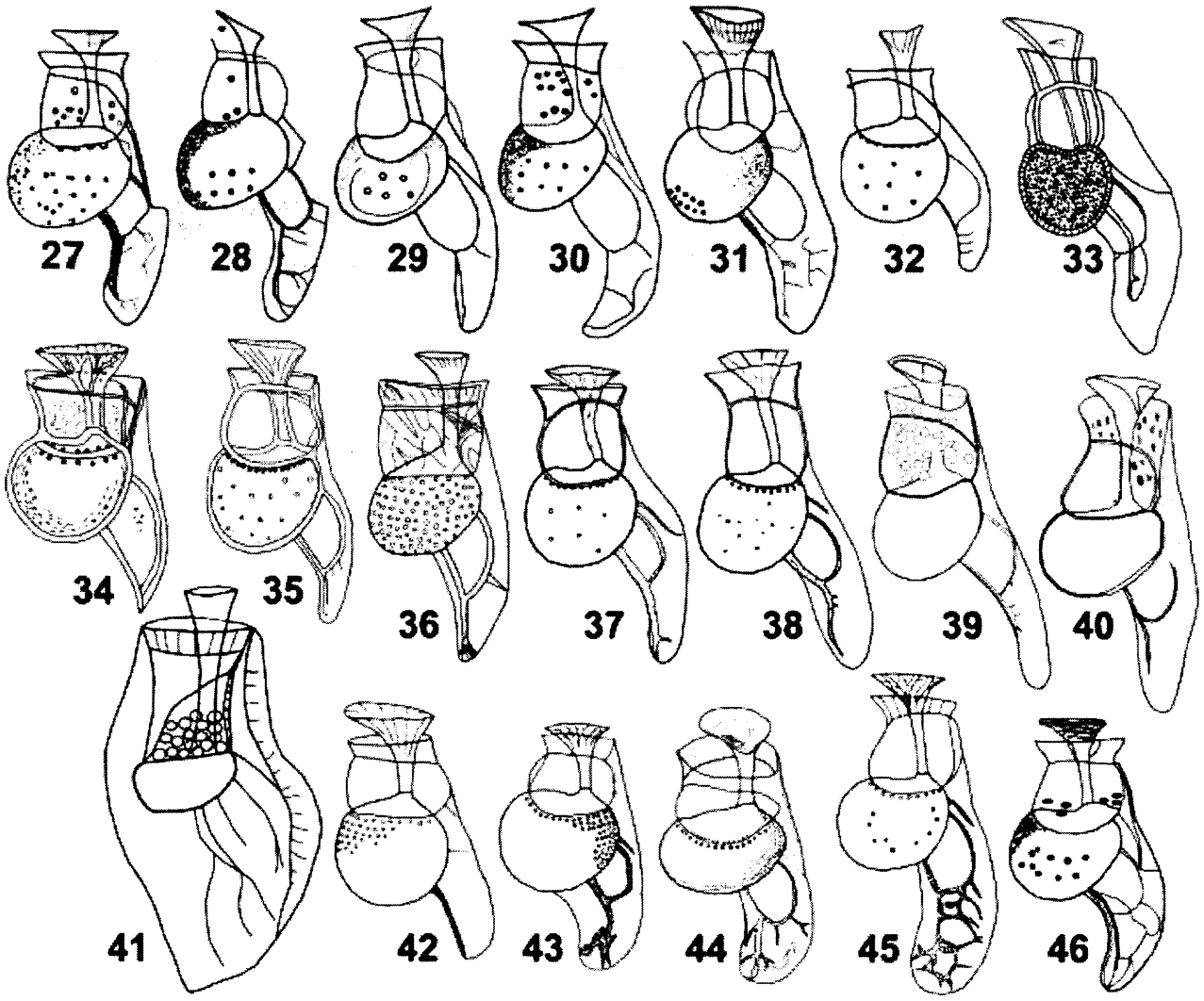


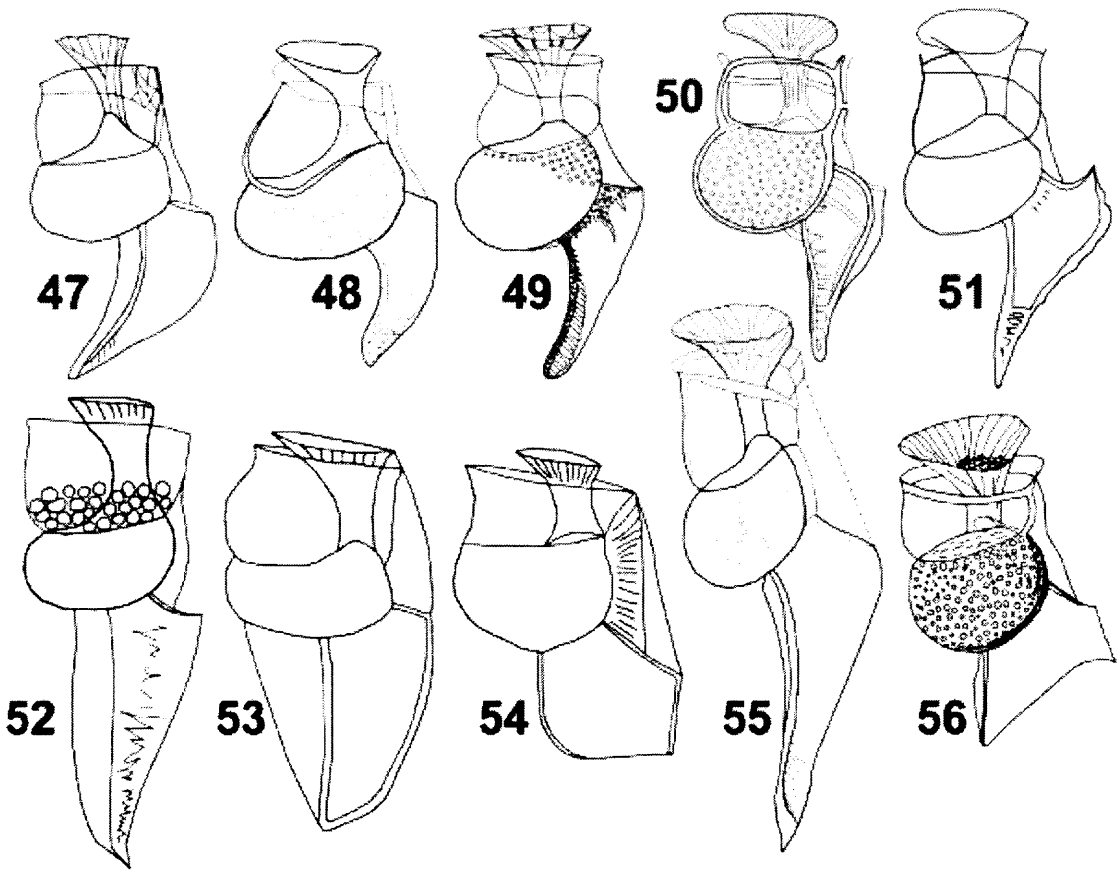
Fig. 1. Descriptive terminology of *Histioneis* in right lateral view.



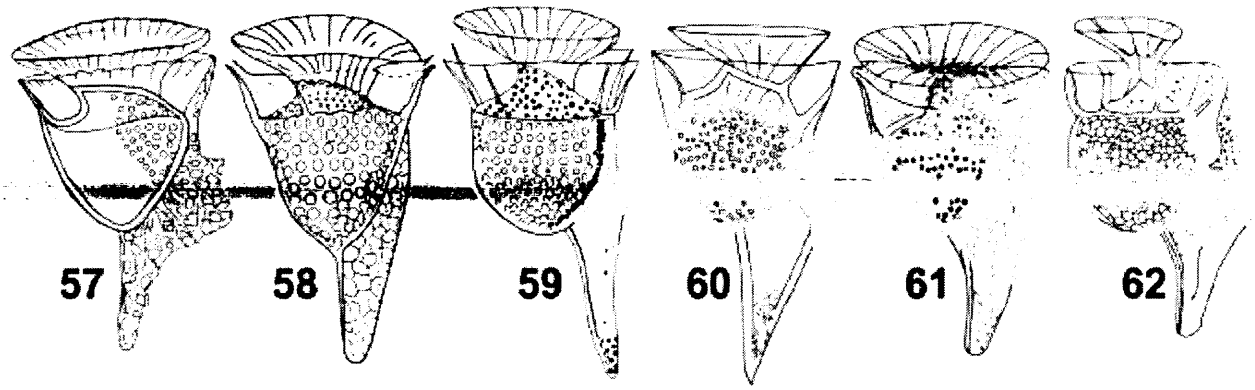
Figs 2-26. Line drawings adapted from the original descriptions of the species morphologically related to the *Histioneis cymbalaria*-group in right lateral view. (2) *H. bougainvillae*. (3) *H. cymbalaria* sec Stein (1883) and *H. skogsbergii* sec Schiller (1933). (4) *H. depressa* sec Wood (1963). (5) *H. depressa* sec Taylor (1976). (6) *H. cymbalaria* sec Stein (1883) and synonym of *H. hyalina* for Kofoid and Skogsberg (1928). (7) *H. depressa*. (8) *H. hyalina* sec Wood (1963). (9) *H. hyalina*. (10) *H. depressa* sec Rampi and Bernhard (1980). (11) *H. speciosa*. (12) *H. cymbalaria* sec Stein (1883). (13-15) *H. cymbalaria* sec Balech (1988). (16) *H. cleaveri*. (17) *H. rampii*. (18) *H. robusta*. (19) *H. panda*. (20) *H. panaria*. (21) *H. pietschmannii*. (22) *H. pulchra*. (23) *H. mitchellana*. (24) *H. schilleri*. (25) *H. detoni*.



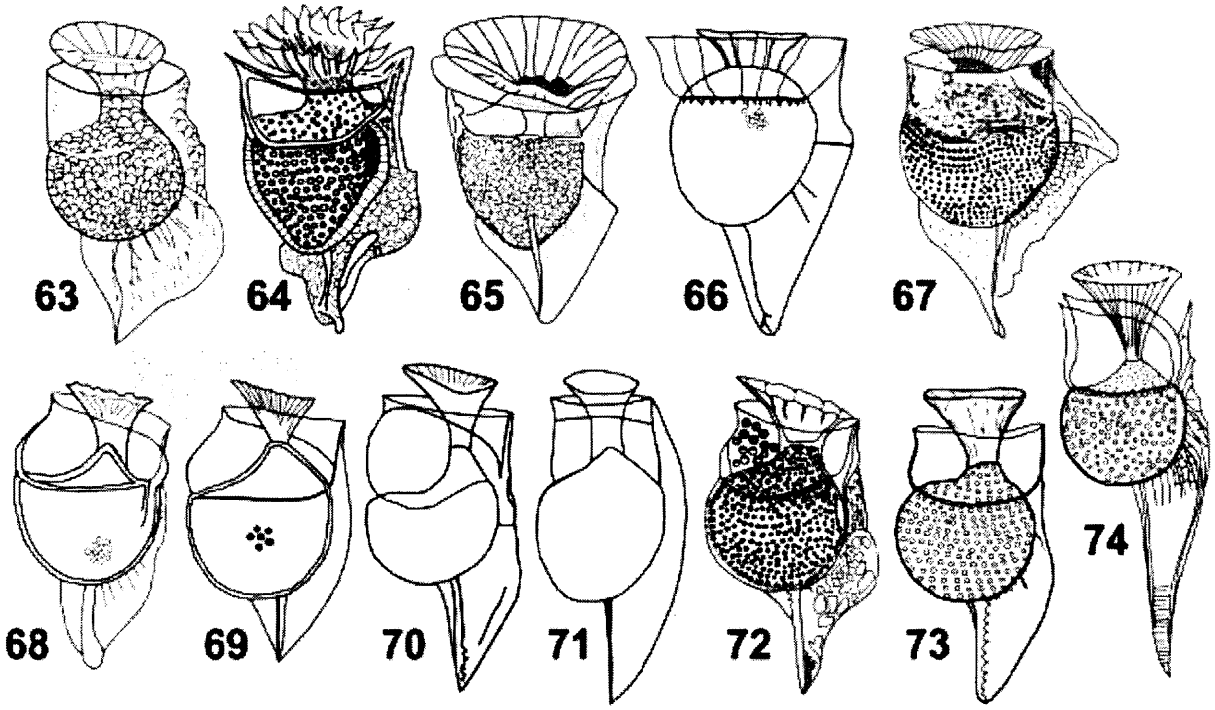
Figs 27-46. *Histioneis longicollis*-group. (27) *H. villafranca*. (28) *H. elegans*. (29) *H. longicollis* sec Halim (1960). (30) *H. sublongicollis*. (31) *H. faouzii*. (32) *H. minuscula*. (33) *H. kofoidii*. (34) *H. vouckii*. (35) *H. joergensenii*. (36) *H. planeta*. (37) *H. joergensenii* sec Rampi and Bernhard (1980). (38) *H. longicollis* sec Rampi and Bernhard (1980). (39) *H. longicollis*. (40) *H. longicollis* sec Schiller (1933). (41) *H. aequatorialis*. (42) *H. marchesonii* (43) *H. bernhardii*. (44) *H. pacifica*. (45) *H. pavillardii*. (46) *H. imbricata*. Not to scale.



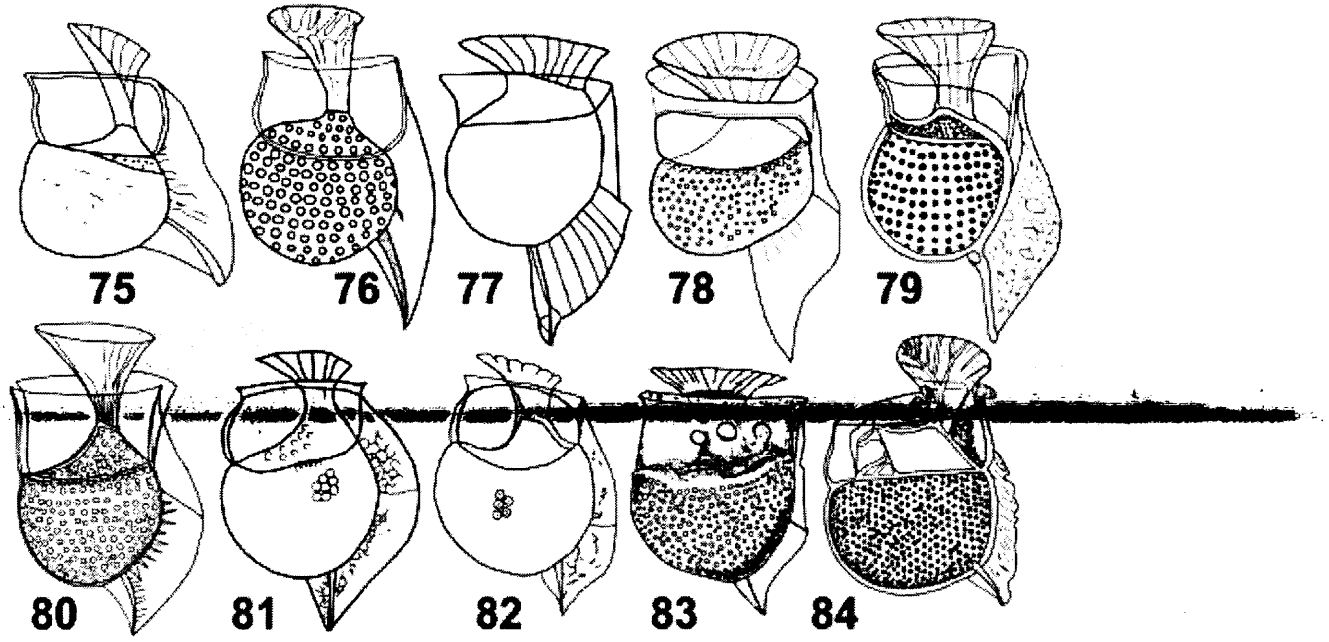
Figs 47-56. *Histioneis elongata*-group. (47) *H. elongata* var. *curvata*. (48) *H. carinata*. (49) *H. subcarinata*. (50) *H. isselii*. (51) *H. elongata* sec Böhm (1936). (52) *H. lanceolata*. (53) *H. australiae*. (54) *H. moresbyensis*. (55) *H. elongata*. (56) *H. costata*. Not to scale.



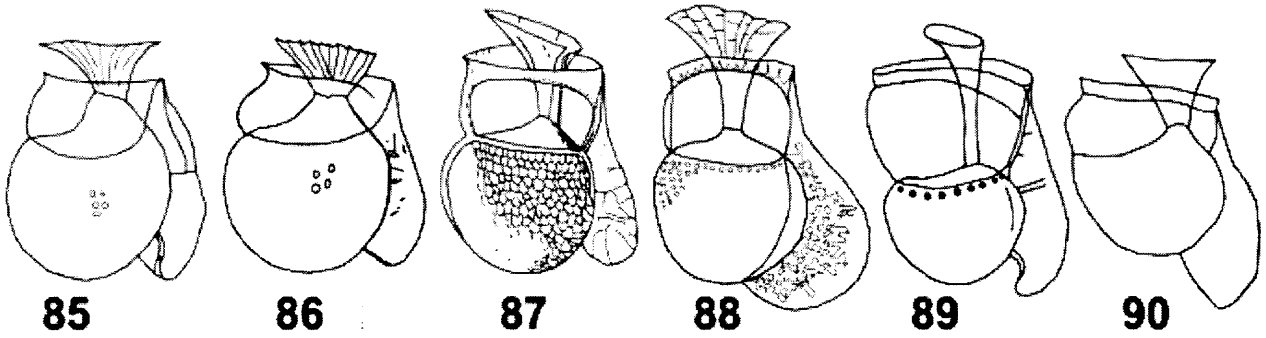
Figs 57-62. *Histioneis para*-group. (57) *P. conica*. (58) *H. para*. (59) *H. paraformis*. (60) *H. acuta*. (61) *H. paraformis* sec Kofoid and Skogsberg (1928). (62) *H. rotundata*. Not to scale.



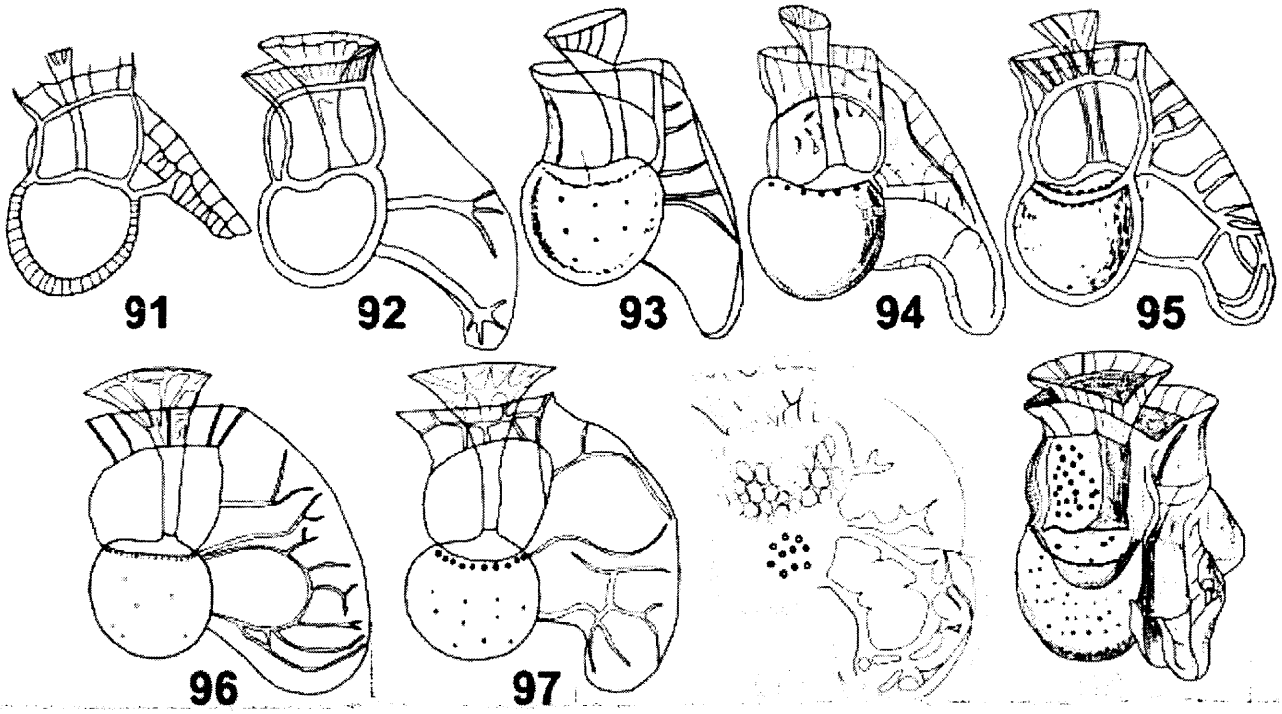
Figs 63-74. *Histioneis garrettii*-group. (63) *H. karstenii*. (64) *H. dentata*. (65) *H. garrettii*. (66) *H. garrettii* sec Balech (1988). (67) *H. diomedeae*. (68) *P. pachypus*. (69) *P. varians*. (70) *H. gregoryi*. (71) *H. tubifera*. (72) *P. pieltainii*. (73) *P. sphaeroidea*. (74) *H. remora*. Not to scale.



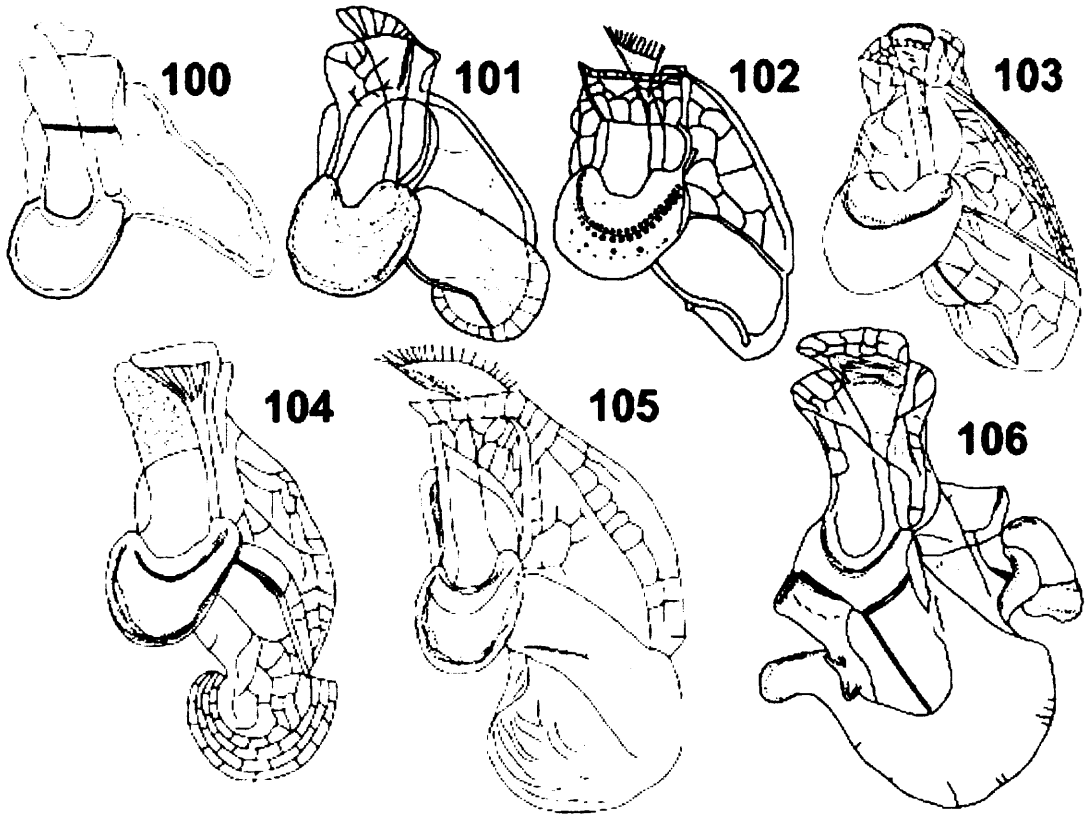
Figs 75-84. *Histioneis crateriformis*-group. (75) *H. diamantinae*. (76) *P. acutiformis*. (77) *P. gascoynensis*. (78) *H. paulsenii*. (79) *H. oxypteris*. (80) *H. crateriformis*. (81) *H. reticulata* sec Balech (1988). (82) *H. crateriformis* sec Balech (1988). (83) *H. reticulata*. (84) *H. mediterranea*. Not to scale.



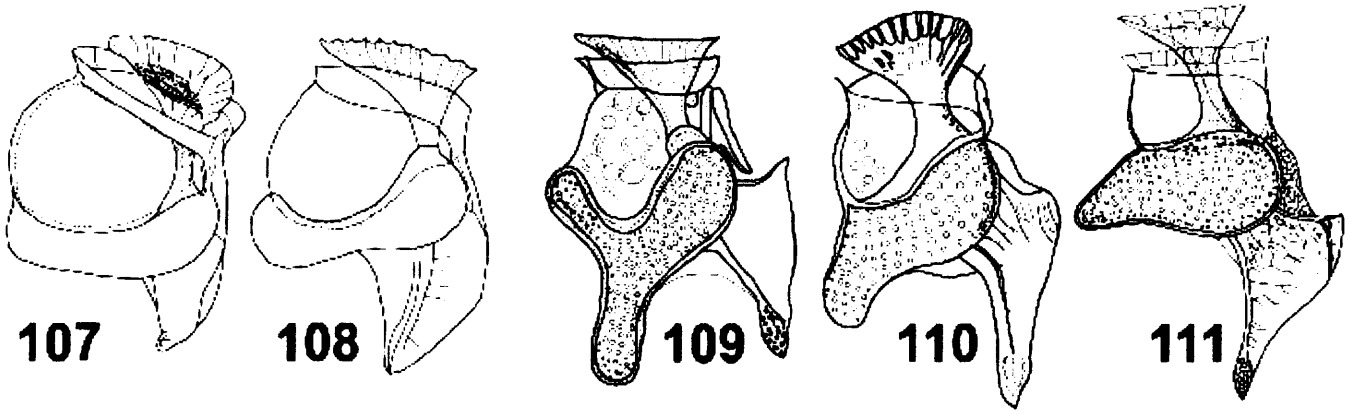
Figs 85-90. *Histioneis inclinata*-group. (85) *H. mediterranea* sec Rampi and Bernhard (1980). (86) *H. dubia*. (87) *H. inclinata*. (88) *H. alata*. (89) *H. inornata*. (90) *H. simplex*. Not to scale.



Figs 91-99. *Histioneis gubernans*-group. (91) *H. fragilis*. (92) *H. cerasus*. (93) *H. parallela*. (94) *H. striata*. (95) *H. variabilis*. (96) *H. ligustica*. (97) *H. expansa*. (98) *H. gubernans*. (99) *H. reginella*. Not to scale.



Figs 100-106. *Histioneis megalocopa*-group. (100) Unidentified specimen illustrated by Sournia (1986, p. 153). (101) *H. helenae*. (102) *H. milneri*. (103) *H. hippoperoides*. (104) *H. megalocopa*. (105) *H. dolon*. (106) *H. josephinae*. Not to scale.



Figs 107-111. Line drawings adapted from the original descriptions in right lateral view. (107) *H. navicula*. (108) *H. oceanica*. (109) *H. highleyi*. (110) *H. biremis*. (111) Unidentified specimen illustrated by Ojeda (1999). Not to scale.

4. Discusión

4.1 Diversidad y biogeografía

4.1.1. ¿Cuántas especies?

En términos de riqueza de especies, los dinoflagelados son sólo comparables con las diatomeas en el medio marino. Sournia *et al.* (1991) en su artículo *Marine phytoplankton: how many species in the world oceans?* no proporciona una lista de especies, pero propone 1424-1772 especies y 115-131 géneros de dinoflagelados libres marinos. Los valores mayores consideran a las especies y géneros de dudosa validez. Otros autores dan valores de 4000 especies de dinoflagelados, donde la mitad de las especies son fósiles (Taylor, 1987), pero ningún trabajo proporciona una lista reciente de especies. En la bibliografía pueden encontrarse inventarios de especies como la revisión de Schiller (1931-1937) que describe e ilustra casi todos los dinoflagelados conocidos en aquel tiempo. Sournia (1973, 1978, 1982a, 1990, 1993) añade listados en orden alfabético de las especies descritas tras la revisión de Schiller.

Según esta memoria de tesis actualizada hasta el año 2004, los dinoflagelados marinos libres conocidos constituyen un total de 1555 especies, distribuidas en 117 géneros. Los géneros más numerosos son: *Protoperidinium* (264 especies), *Gymnodinium* (173 especies), *Dinophysis+Phalacroma* (104+41 especies), *Gyrodinium* (87 especies), *Amphidinium* (76 especies), *Histioneis* (65 especies), *Ceratium* (64 especies) y *Gonyaulax* (60 especies) (Fig. 15). Desde 1993 hasta 2004, se han descrito 135 nuevas especies así como los nuevos géneros: *Akashiwo*, *Amphidiniella*, *Bysmatrum*, *Gaarderia*, *Heterobractum*, *Karenia*, *Karlodinium*, *Lessardia*, *Mysticella*, *Plagiodinium*, *Polarella* y *Takayama.*

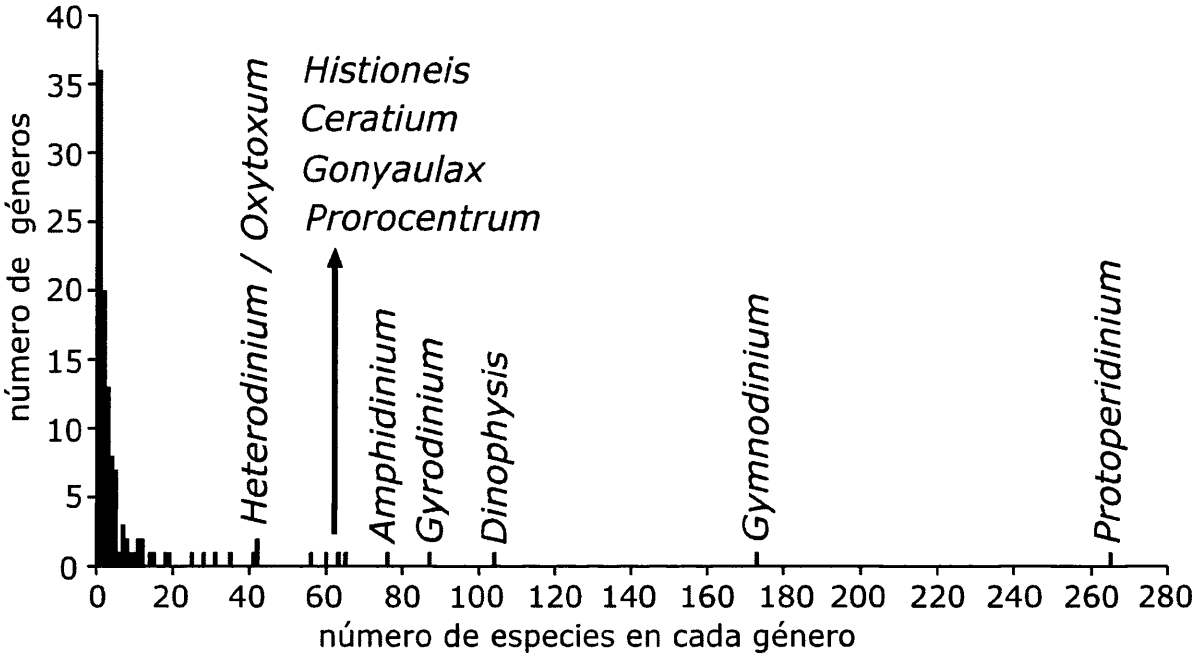


Fig. 15. Distribución de frecuencia del número de especies en cada género basado en Gómez (2005).

De los 2500 nombres de especies de dinoflagelados marinos aparecidos en la bibliografía, unos 1000 nombres de especies han sido considerados como sinónimos de especies ya descritas. Sin embargo, si analizamos los géneros más importantes, el número de especies válidas conocidas podría ser aún menor.

Protoperidinium con 264 especies es el género más numeroso (Fig. 15). Balech transfirió la mayor parte de las especies marinas de *Peridinium* a *Protoperidinium* en 1974, y además describió un total de 100 nuevas especies. Abé (1981) describió otras 40 especies nuevas. Tanto Balech como Abé se basaron en pequeñas diferencias en la tabulación, principalmente de las placas sulcales para crear estas nuevas especies. Nadie ha vuelto a realizar estos minuciosos estudios y la mayor parte de las especies descritas por ambos autores no han vuelto a ser citadas. No hay estudios sobre la variabilidad intraespecífica de las placas sulcales. La cuestión está en si mínimas diferencias en la forma de las placas sulcales justifican la separación como diferentes especies o al contrario, existe una especiación críptica y una misma morfología encierra diferentes especies.

Al ser *Protoperidinium* un género heterotrófico, su cultivo es aún más difícil que en el caso de especies autótrofas y por tanto la variabilidad morfológica, al menos en condiciones de laboratorio, es difícil de estudiar. La biología molecular

podría ayudar, pero a pesar de lo relativamente fácil que resulta capturar estas especies generalmente grandes y resistentes, hasta el presente sólo se conocen 10 secuencias parciales de las 264 especies de *Protoperidinium* descritas (Yamaguchi y Horiguchi, 2005). Por tanto es aún prematuro evaluar la validez de las especies del género de dinoflagelados más numeroso.

Gymnodinium es el segundo género más numeroso, que incluye a muchos *Gyrodinium* y en algunos casos descripciones de *Amphidinium* que corresponden a especies de *Gymnodinium* giradas 180°. Ambos, *Gymnodinium* y *Gyrodinium* tienen un cíngulo ecuatorial, pero Kofoid y Swezy (1921) los separaron, al asignar al género *Gyrodinium* las especies en las que los extremos del cíngulo estaban desplazados más del 1/5 de la longitud del cuerpo celular. Evidentemente este criterio es arbitrario y en modo alguno tiene una base filogenética. La mayor parte de las especies atecadas fueron descritas a finales del siglo XIX y principios del XX a partir de especimenes fijados, lo que altera drásticamente su morfología, y además en muchos casos descritos a partir de un único espécimen. Incluso aunque se observen individuos aún vivos, se sabe que la morfología cambia rápidamente tras su captura (Kofoid y Swezy, 1921).

Es muy probable que muchos de esos dinoflagelados descritos a partir de una sola célula correspondan a un espécimen deformado de una especie ya conocida. Los dinoflagelados atecados son a menudo heterótrofos y tras expulsar los restos de la presa que han ingerido, presentan un contorno muy deformado y variable, que puede haber llevado a que se les describa como especies diferentes. Un ejemplo se puede encontrar en *Gyrodinium spirale*. Schütt (1895) describió numerosas variedades de *Gyrodinium spirale* y después Kofoid y Swezy (1921) dieron categoría de especie a *Gyrodinium acutum*, *G. cornutum*, *G. mitra*, *G. obtusum* o *G. pingue*. También *Gyrodinium fusiforme*, *G. lachryma* o *G. nasutum* pueden no ser más que variedades de *Gyrodinium spirale*.

Más del 80% de las especies de dinoflagelados atecados descritos por Kofoid y Swezy (1921) no han sido citadas por otro autor y el porcentaje es aún mayor en géneros como *Warnowia*. Para investigar la validez de las especies, una solución pasa por aislar la especie en la localidad tipo, pero como ocurre con las especies descritas por Schütt, ni siquiera se conoce la localidad tipo. La descripción de más de un centenar de especies de estos géneros es claramente insuficiente. En 1985 Haruyoshi Takayama usando microscopía electrónica de barrido ilustra varios tipos de surco apical en especies atecadas. Este carácter

morfológico, junto la composición pigmentaria y diferencias en la secuencia del rADN han justificado la escisión del macro-género *Gymnodinium* (Daugbjerg *et al.*, 2000). Sin embargo, las especies investigadas son sólo aquellas disponibles en cultivos y poco se sabe sobre en el ciclo de vida y morfología de esas especies en condiciones naturales.

Tras *Protoperidinium* y *Gymnodinium*, el género más numeroso es *Dinophysis*. *Phalacroma* es a menudo considerado sinónimo de *Dinophysis*, pero al desconocerse la especie tipo de *Phalacroma* es difícil resolver la cuestión. Tan sólo algunas especies costeras del género *Dinophysis* causantes de episodios tóxicos han sido investigadas, manteniéndose en cultivo por algunas generaciones, lo suficiente como para mostrar una alta variabilidad morfológica (Reguera *et al.*, 1995). Una de las especies más comunes en costas atlánticas europeas, *Dinophysis acuminata*, ha recibido hasta diez nombres diferentes. Estos cambios morfológicos no sólo ocurren en Dinophysiales, y no sólo debido a cambios en el ciclo de vida. Condiciones ambientales como los niveles de turbulencia son responsables de cambios en la morfología. Un trabajo publicado por Zirbel *et al.* (2000) sirve como ejemplo para ilustrar la gran variabilidad morfológica (Fig. 16).

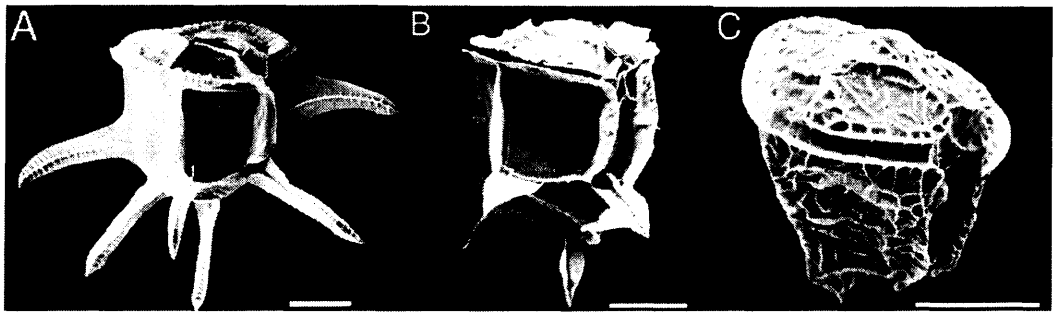


Fig. 16. Morfología de células de *Ceratocorys horrida* cultivadas a diferentes niveles de turbulencia en Zirbel *et al.* (2000).

Podría pensarse en la fig. 16 se ilustran tres especies diferentes, sin embargo es la misma especie e incluso la misma cepa de *Ceratocorys horrida*. Las tres formas coexisten en cultivos y pueden cambiar de una morfología a otra en cuestión de minutos, tan sólo si se cambian los niveles de turbulencia. Eso ocurre en una especie fuertemente tecada como *Ceratocorys*, pero la versatilidad morfológica puede ser aún mayor en células atecadas. El conocimiento de la variabilidad morfológica de *Dinophysis* esta restringida a una docena de especies

de costas templadas o boreales, nada se sabe de la variabilidad de los cientos de especies de Dinophysiales descritas en aguas abiertas tropicales como *Histioneis* o *Amphisolenia*, en su mayor parte descritas a partir de la observación de un solo ejemplar, ¿es justificable en estos casos que pequeñas diferencias en la aleta sulcal o en las espinas antapicales sean criterio válido para considerarlas como especies diferentes?. Es una incógnita el número de especies de Dinophysiales válidas en aguas oceánicas.

Una gran parte de las nuevas especies descritas en los últimos 15 años son bénticas, como en el caso de *Prorocentrum* (Faust, 1993; Hoppenrath, 2000). Es posible que el aislamiento en ambientes bénticos favorezca una mayor especiación frente a las especies planctónicas. La aplicación de la microscopía electrónica a aguas tropicales lleva a Carbonell-Moore (1993) a describir a partir de muestras de red decenas de especies de podolampadaceas, que debido a su baja densidad y escasos caracteres distintivos pasaban desapercibidas. Poco se sabe de las abundantes especies atecadas en aguas abiertas de mares tropicales.

Si se excluyen todas estas especies dudosas por ser probablemente parte del ciclo de vida de otras especies ya conocidas, el número de especies de dinoflagelados válidas se quedaría en torno a medio millar de especies, de las cuales apenas se conocen secuencias del ADN ribosómico de 100 especies marinas.

Cuantas de las especies descritas de dinoflagelados son válidas es difícil de saber. Esta memoria no puede responder a esa pregunta, pero proporciona un inventario de las especies conocidas, incluyendo los sinónimos más comúnmente aceptados y correcciones en la nomenclatura según el Código botánico vigente. La clasificación usada evita un simple listado alfabético, pero está a la espera que la filogenia molecular llegue al menos a algún representante de cada grupo y se pueda realizar una nueva clasificación de las especies conocidas.

Gómez, F., 2005. A list of dinoflagellates in the world oceans. *Acta Botanica Croatica* 64, 129-212.

4.1.2 Biogeografía

La biogeografía se define como las observaciones, registro y explicación de los rangos de distribución geográfica de los organismos (Pielou, 1979). Los primeros estudios en aguas oceánicas llevaron a Haeckel o Schütt (1897) a considerar que cada masa de agua estaba caracterizada por su plancton-flora propia. P.T. Cleve (1903, p. 7) llegaba a designar cada tipo de agua con el nombre de la especie principal de plancton. Por ejemplo 'Tripos-plankton' para un tipo de agua donde dominada por *Ceratium tripos*. De esta forma se buscaba usar las especies como indicadores biológicos, aportando datos complementarios a la hidrografía. A medida que se amplió la cobertura geográfica de los estudios, se observaba que las especies aparecían en diferentes océanos y por tanto dejaba de tener sentido considerar que cada masa de agua tuviese su plancton endémico.

En general se considera que los organismos de pequeño tamaño son muy abundantes y se pueden dispersar fácilmente, especialmente en un medio sin aparentes barreras físicas como los océanos. Esto ha llevado a asumir que los microorganismos tienen una distribución cosmopolita (Finlay, 2002). Beijerinck basándose en cultivos de bacterias afirma 'todo esta en todas partes, el medio selecciona' (Beijerinck, 1913). Por tanto si se dan las condiciones apropiadas, una especie de microorganismo aparecerá en cualquier lugar.

De estas ideas surgen dos corrientes:

1) todos los microorganismos tienen una distribución cosmopolita, con un bajo grado de endemismo y bajo número de especies (Finlay *et al.*, 1996; Fenchel *et al.*, 1997). Por tanto existirían grandes poblaciones de cada especie de microorganismo y una gran probabilidad de dispersión que previene el aislamiento y la especiación alopátrica (Fenchel *et al.*, 1997);

2) existe un gran endemismo y quedarían muchas especies de protistas por describir, pero las especies no son fáciles de diferenciar (Foissner, 1999). En esta última década, el desarrollo biología molecular debería clarificar una la importancia de la especiación críptica. En estos microorganismos el concepto de especie no tiene en el mismo sentido que conocemos en animales superiores.

Mientras que para microorganismos acuáticos epicontinentales pueden existir barreras físicas que separen a sus poblaciones, más difícil es encontrar claras barreras en aguas oceánicas. Los estudios sobre la biogeografía del fitoplancton han sido escasos. Smayda (1958) se centra en la re-definición de los términos

usados en la biogeografía del fitoplancton y tan sólo cita algunos ejemplos, especialmente de diatomeas bipolares. Margalef (1961), basándose en la bibliografía de que disponía, separa las especies de fitoplancton mejor conocidas en 12 grupos en función de su distribución geográfica. La mayor parte de las especies resultaban cosmopolitas. Hoy en día, 45 años tras el trabajo de Margalef, muchas de aquellas especies señaladas como exclusivamente australes o boreales, Indo-Pacíficas o atlánticas has sido citadas en otras regiones y por tanto el porcentaje de especies cosmopolitas es aún mayor, siempre asumiendo que las identificaciones han sido correctas.

Evidentemente no todos los protistas son cosmopolitas, algunas especies están restringidas a zonas climáticas particulares. Por ejemplo el género *Histioneis* esta asociado con aguas cálidas. La morfología de *Histioneis* ha evolucionado hasta crear una cámara para albergar cianobacterias simbiontes que fijan nitrógeno (Foster *et al.*, 2006) y le proporcionan alimento adicional. La fijación de nitrógeno se inhibe a bajas temperaturas, así que la distribución de *Histioneis* se limita a aguas cálidas. También muchas podolampadaceas parecen restringidas a aguas cálidas (Carbonell-Moore, 1996). En aguas superficiales tropicales, las especies de género *Pyrocystis* parecen constituir una excepción. Ninguna asociación simbiótica ha sido descrita en la especie y sin embargo, *Pyrocystis pseudonoctiluca*, una especie aparentemente autótrofa, es común en aguas oceánicas tropicales. Este fenómeno se explica por migraciones verticales que le permiten explotar nutrientes de aguas profundas, que tan sólo especies de gran tamaño como *Pyrocystis* pueden realizar (Sukhanova y Radyakov, 1973).

En el lado opuesto a las especies pantotropicales, estarían las especies polares (Balech, 1976; Okolodkov y Dodge, 1996). Sin embargo, tampoco puede descartarse que en algún caso se trate de especies cosmopolitas que modifican su morfología en condiciones extremas. La diversidad de dinoflagelados en aguas polares es escasa comparada con los trópicos. A parte de las bajas temperaturas, sólo especies que formen quistes o heterótrofas pueden adaptarse a los largos periodos de oscuridad en regiones polares. Existe un gran número de dinoflagelados heterótrofos como *Protoperidinium*, que son aparentemente unipolares, simplemente porque E. Balech trabajó en aguas antárticas (Balech, 1976). Si Balech hubiese analizado muestras del Ártico, muchas de esas especies serían bipolares. Por ejemplo en 1999 se descubrió el género *Porallela* en el océano Antártico, hasta entonces era sólo conocido en el registro fósil. Como es

un género de interés, se investigó su presencia en el Ártico y rápidamente se encontró (Montresor *et al.*, 2003). *Porallela glacialis* es la misma especie en ambos polos y apenas difiere en 6 pares de bases en su SSU rADN (Montresor *et al.*, 2003). En principio se puede considerar que las especies bipolares tuvieron una distribución cosmopolita en periodos más fríos y que el progresivo calentamiento redujo su distribución a los polos. Es difícil asumir que en la actualidad una especie psicrófila pueda trasladarse de un polo a otro, especialmente las especies fotosintéticas que deberían resistir a las altas temperaturas en la zona iluminada de los trópicos. Una divergencia genética muy lenta surge como explicación a este fenómeno.

Las especies del género *Ceratium*, generalmente grandes y resistentes, fácilmente retenidas por muestras de red y relativamente bien identificables, han sido comúnmente usadas como indicadores biogeográficos (Dodge y Marshall, 1994). Especies como *Ceratium* (*longipes*) *arcticum* están restringidos a aguas frías y otras como *Ceratium dens/divaricatum/balechii* parecen restringidas a aguas costeras tropicales. Sin embargo, la delimitación de las especies de *Ceratium* es complicada por la gran variabilidad intra-específica que presenta.

Por regla general las especies oceánicas tienden a ser heterótrofas, mixotrófas o presentan simbiónte̲s. Por ejemplo, en las aguas ultraoligotróficas del Giro del Pacífico Sur, las especies más abundantes pertenecen al género *Oxytoxum* y especies de *Ceratium* como *C. teres*. En aguas oceánicas, las especies tienden a ser más ornamentadas como en el caso de la Dinophysiales, mientras que las especies neríticas de este orden son menos ornamentadas. Además de una relación con el grado de turbulencia y tasa de sedimentación (Zirbel *et al.*, 2000), la ornamentación puede estar destinada a modular corrientes de aguas que dirigen a sus presas hacia la región sulcal, generalmente presas de pequeño tamaño como el picoplancton. Las Dinophysiales de aguas costeras donde los nutrientes permiten vida autótrofa carecen de esta ornamentación.

La separación entre especies de afinidad nerítica (parácticas) y oceánica (anoicticas), más que geográfica, es una separación entre condiciones eutróficas que predominan en las costas frente a la general oligotrofia en aguas oceánicas. La formación de quistes es una ventaja para las especies neríticas, porque un quiste que sedimenta en aguas oceánicas difícilmente podría volver a la zona fótica. La ocurrencia de especies coloniales en aguas abiertas es rara, mientras

que es más común en especies neríticas como *Alexandrium*, *Pyrodinium bahamense* o pseudo-coloniales como *Polykrikos*. La velocidad de desplazamiento podría ser mayor cuando las células están unidas formando colonias, facilitando las migraciones verticales o también podría incidir en la tasa de mortalidad por depredación. En aguas oceánicas, aunque la formación de colonias incrementase la velocidad de ascenso y descenso, la distancia hasta la nutriclina sería tan grande, a menudo más 200 m, que las especies requerirían grandes vacuolas y varios días para completar el ciclo.

Algunas especies autótrofas parecen adaptadas a vivir en aguas profundas. Sournia (1982b) en su estudio de la "*schatten flora*" no encuentra una morfología común entre las especies de aguas profundas. Es esperable que las especies autótrofas en aguas profundas requiriesen una mayor concentración de pigmentos y otras adaptaciones como cuerpo y extensiones aplanadas como en el caso de *Ceratium platycorne*, *C. ranipes* o *C. praelongum*.

Los ejemplos de endemismo en aguas tropicales y templadas son escasos. Las poblaciones oceánicas de dinoflagelados han estado interconectadas hasta la formación del istmo de Panamá hace tan sólo 6 millones de años. Algunas especies aparecen restringidas a la región Indo-pacífica. *Dinophysis miles*, una especie que no puede dar ninguna duda en su identificación, parece restringida a las costas tropicales del Índico y el sureste asiático. Sólo en esta región del sureste asiático, la cosmopolita *Noctiluca scintillans* presentan simbiontes, *Pedinomonas noctilucae*. Realmente no podemos asegurar que estas especies estén limitadas a aguas tropicales del Índico o Pacífico, porque áreas tropicales como el Golfo de Guinea están casi inexploradas. Si parece existir un mayor grado endemismo en microorganismos que son estrictamente autótrofos como diatomeas. Los dinoflagelados con una mayor versatilidad trófica, gran variabilidad morfológica y una gran diversidad genética, podrían adaptarse mejor a diferentes condiciones ambientales y por tanto tener un mayor rango de distribución.

El estudio de la biogeografía de las especies de dinoflagelados es difícil, incluso cuando se trata de especies fácilmente identificables, debido a la heterogeneidad de los estudios. Así por ejemplo las costas de Europa, Japón y Norte América han sido objeto de más estudios, mientras que vastas regiones de aguas abiertas de mares tropicales y especialmente del hemisferio sur han sido escasamente investigadas. Muchas especies que se citan en trabajos, no son

ilustradas o las ilustraciones no son suficientemente detalladas como para confirmar la identificación y por tanto no se pueden sacar conclusiones claras sobre la distribución geográfica de las especies.

En la presente memoria se ha estudiado la composición de especies en regiones históricamente bien estudiadas como la Costa Azul o el Canal de la Mancha y también otras zonas poco conocidas como aguas abiertas del sudeste asiático y el océano Pacífico central y Sur. Por ejemplo, en el océano Pacífico que ocupa 1/3 de la superficie de los océanos, géneros muy distintivos como *Asterodinium*, *Brachidinium*, *Microceratium*, *Ceratoperidinium*, *Scaphodinium*, *Petalodinium*, *Pomatodinium*, *Leptodiscus* y *Spatulodinium*, nunca habían sido citados. Por tanto géneros como *Ceratoperidinium* o *Petalodinium* serían endémicos del mar Mediterráneo sin los estudios incluidos en esta memoria. El carácter endémico de estas especies tan sólo depende de que los escasos investigadores en activo y con la experiencia suficiente para identificar a esos grupos investiguen nuevas áreas geográficas. *Scaphodinium*, aparece en cualquier localización desde el sur de Japón a Chile, pero nunca había sido citado en el Pacífico.

El Mediterráneo por sus características de aislamiento, pero conectado en las regiones atlánticas e Indo-pacífica es un buen laboratorio para estudios biogeográficos. Son muchas las especies macroscópicas claramente endémicas de aguas mediterráneas o especies de un claro origen Indo-Pacífico (Bianchi y Morri, 2000). Sin embargo cuando se estudia la afinidad biogeográfica en especies de dinoflagelados, no es posible encontrar una especie que se pueda usar como un claro ejemplo de especie endémica o Indo-pacífica.

Por ejemplo, surge la duda si es la misma especie un *Ceratoperidinium* de la Bahía de Palma recogido en aguas con una temperatura de 14°C o en aguas abiertas del Pacífico ecuatorial a 29°C. No existen diferencias en la morfología basado en microscopía óptica. De momento hay que esperar a que los estudios genéticos se extiendan a aguas abiertas oceánicas y así descartar una especiación críptica y que bajo la misma morfología tengamos especies diferentes en cada región oceánica.

Es esperable que exista un mayor porcentaje de especies endémicas en las cuencas cerradas o semicerradas. El Mar Mediterráneo cumple estas características y ha sido una de las regiones históricamente mejor investigada, citándose al menos la mitad de especies conocidas de dinoflagelados. Al ser un

mar casi cerrado, con múltiples regímenes climáticos e hidrológicos, una compleja historia geológica con episodios de conexiones y aislamiento con los océanos Atlántico e Indo-Pacífico, el Mediterráneo se presenta como un área ideal para estudio la biogeografía de los dinoflagelados marinos. Tras un inventario de las especies descritas en las cuencas del Mediterráneo y Mar Negro, esta memoria ha tratado de responder a cuestiones como el número de especies endémicas o Indo-Pacíficas que podemos encontrar en el Mediterráneo.

Gómez, F., 2003. Checklist of Mediterranean free-living dinoflagellates. *Botanica Marina* 46, 215-242.

Gómez, F. y Boicenco, L., 2004. An annotated checklist of dinoflagellates in the Black Sea. *Hydrobiologia* 517, 43-59.

Gómez, F., 2006. Endemic and Indo-Pacific plankton in the Mediterranean Sea: A study based on dinoflagellate records. *Journal of Biogeography* 33, 261-270.

4.2 Taxonomía y distribución de grupos de dinoflagelados poco conocidos

Existe una gran heterogeneidad en el estudio de la diversidad de dinoflagelados. Aquellas especies que pueden causar daños en las costas como puede ser el caso de *Karenia brevis* reciben multitud de fondos para su estudio, mientras que ordenes enteros como los Noctilucales (excluyendo *Noctiluca*), a pesar de interés en la evolución de los dinoflagelados, no han recibido ninguna atención en las últimas tres décadas.

Cada época se ha caracterizado por diferentes recursos a la hora de investigar la taxonomía de las especies. En los últimos 10 años, predominan los estudios basados en un solo espécimen aislado durante una proliferación costera y cultivado en condiciones de laboratorio, que raramente reproducen las condiciones naturales. El abundante material permite aplicar los últimos adelantos técnicos disponibles. Las especies son descritas combinando microscopía óptica, epifluorescencia, microscopía electrónica de barrido y transmisión, perfiles de pigmentos y a veces de toxinas, y además la secuencia de regiones del ADN ribosómico. Estas técnicas raramente se aplican a los dinoflagelados de aguas abiertas sobre todo en mares tropicales, alejados de los principales laboratorios.

Cuando tan sólo se dispone de la microscopía óptica clásica es difícil realizar estudios taxonómicos que alcancen los requerimientos de las revistas más reconocidas en la actualidad. En este contexto, la falta de recursos se debe suplir incrementando el esfuerzo en la observación, hasta llegar a encontrar especies muy poco conocidas y que sean tan interesantes que incluso tan sólo con microscopía óptica los resultados sean competitivos. No es especialmente necesario irse muy lejos para encontrar especies de interés. Por ejemplo, *Ceratoperidinium* es casi desconocido, pero se pueden encontrar especimenes en otoño cogiendo un cubo de agua en las orillas de la Bahía de Palma de Mallorca. *Spatulodinium pseudonoctiluca*, uno de los pocos dinoflagelados presentes en el Canal de la Mancha, tiene un ciclo de vida curioso y poco conocido, pero no recibe ningún interés. Evidentemente siempre se tienen mayores posibilidades de encontrar especimenes interesantes en las áreas más remotas, como puede ser aguas abiertas mares tropicales de Asia, el Pacífico Central o el Giro del Pacífico Sur.

Hoy en día es difícil que tan sólo un estudio taxonómico interese a las Instituciones que financian estos costosos muestreos en aguas abiertas, de forma que el análisis de las muestras también debe contribuir en aspectos ecológicos del fitoplancton, más útiles para estudios biogeoquímicos que financian las campañas en aguas abiertas. Incluso en las regiones más remotas, se han realizado estudios con muestras de red que permiten recolectar millones de especimenes, en su mayor parte ya estudiados incluso por microscopía electrónica. Aquellos especimenes de menor tamaño, que no son retenidos por la red de plancton o bien especimenes de mayor tamaño, pero tan delicados que se destruyen durante el filtrado, han sido objeto de menos estudios y por tanto pueden encontrarse especies poco conocidas.

En aguas abiertas donde la abundancia de células es muy baja y sin usar redes de plancton, se utilizan otros métodos de concentración. Es costoso transportar grandes volúmenes de zonas remotas hasta el laboratorio y la sedimentación de grandes volúmenes de agua es laboriosa. Son escasas las ocasiones en que los organismos pueden investigarse a bordo y por lo tanto es necesaria la fijación para su posterior estudio en laboratorio. Tras una laboriosa sedimentación, el resultado permite observar con microscopía invertida, especimenes que normalmente se dañan o escapan de las redes de plancton y entonces raras noctilucaceas o pequeñas células tecadas con delicada ornamentación como *Histioneis* aparecen. Cientos de pequeños especimenes interesantes, principalmente dinoflagelados atecados, son aún más abundantes. Sin embargo debido a su pequeño tamaño, la resolución de la microscopía invertida no permite diferenciar su morfología y sin el auxilio al menos la microscopía electrónica de barrido, estos especimenes han sido descartados para estudios taxonómicos. En plena era de la biología molecular, las publicaciones requieren la secuencia de rARN incluso cuando se dispone de un sólo espécimen, lo cual es casi imposible tratándose de especimenes fijados con Lugol. Si es sencillo, sin embargo, aplicar la técnica desarrollada por el Dr. Takayama para dinoflagelados, que permite observar mediante microscopia electrónica de barrido el espécimen elegido.

Alguna de estas pequeñas células gymnodinioides presenta extensiones y eso permite distinguirla de otras como es el caso de dinoflagelados atecados con extensiones como *Asterodinium*, *Brachidinium*, *Microceratium*, *Ceratoperidinium* y algunos otros no conocidos anteriormente.

4.2.1. *Brachidinium, Asterodinium, Microceratium*

A pesar de alcanzar dimensiones de más de 100 µm y llegar a abundancias de hasta 11000 células por litro al sur de Canarias como encontró Margalef (1975) o Estrada (1976), el género *Brachidinium* no fue descrito hasta 1963 y *Asterodinium* y *Microceratium* hasta 1972. Resulta verdaderamente anormal que se tardara tanto en describir esos géneros tan distintivos. Tan sólo puede explicarse porque los estudios anteriores, generalmente muestras de red fijadas con formol, utilizaban una metodología inapropiada. El exceso de formol en la muestra pudo ser la causa de la descripción incompleta de *Brachidinium* por Taylor (1963). Taylor al no observar ni siquiera el cíngulo, incluyó a *Brachidinium* en el orden Dinoccocales, unos dinoflagelados cocoides o parásitos y carentes de flagelos, lo que dio a *Brachidinium* un halo de misterio. Taylor, sin otras observaciones, continuó en sus libros imaginando la morfología de *Brachidinium* y proponiendo hasta tres orientaciones diferentes erróneas (Taylor, 1963, 1980b, 1987; Fensome *et al.*, 1993).

Sournia observó especimenes de *Brachidinium capitatum* con una morfología variable en las extensiones y describió algunas formas como nuevas especies. En las mismas estaciones donde Sournia encontraba *Brachidinium*, pero a más profundidad, solían aparecer especimenes de *Asterodinium* con el mismo núcleo prominente, una pigmentación verde-amarilla más intensa y extensiones de *Brachidinium*, pero con 5 extensiones en diferente posición y también otro género, *Microceratium*, con sólo 3 extensiones (Sournia, 1972a,b). Por aquel tiempo, Cachon en Villefranche/Mer había observado un espécimen de *Brachidinium* vivo y describió que podía mover sus extensiones (Léger, 1971). Esto lleva a Sournia (1972a) a crear el orden Arthrodiniales 'dinoflagelados articulados' para estos dos géneros. Loeblich (1982) añadiría más confusión creando el orden "Brachydiniales", que sin embargo sería validado por Sournia (1984). Después Taylor (1987, p. 729) incluye a las brachidiniaceas en el orden Kolkwitziellales y poco después en Ptychodiscales (Fensome *et al.*, 1993).

Sournia (1972b), coincidiendo con *Asterodinium* y *Brachidinium* y *Microceratium*, también observó unas células gymnodinioides y anotaba "*poché à* Brachidinium". Sournia (1972b) ilustró lo que en 2004 se describió como *Karenia papilionacea*. En 1986, en su *Atlas du Phytoplancton Marin*, Sournia escribía que los Brachidiniales quizás eran parte ciclo vida de otros dinoflagelados más comunes, sin dar más información.

En una casi inaccesible publicación, Abboud-Abi Saab (1989) encuentra *Brachidinium capitatum* y las mismas células gymnodinioides que ya observó Sournia (1972b). Abboud-Abi Saab incluye una nueva especie, *Asterodinium libanum*, con una pésima fotografía y sin apenas descripción. Poco más se conoce sobre la morfología de los misteriosos Brachidiniales, pero ¿cual es la verdadera naturaleza de estos dinoflagelados?, ¿son realmente tan diferentes como para considerarlos un orden distinto de otros dinoflagelados?

A medida que el número de especimenes observados fue incrementando y los medios técnicos y la experiencia mejoraron, se ha podido llegar a establecer una hipótesis que puede revelar la verdadera naturaleza de esos organismos. Además de los Brachidiniales, otros dinoflagelados producen extensiones en condiciones desfavorables como dos especimenes similares con una distintiva forma de "H".

Gómez, F., 2003. New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae). *Nova Hedwigia* 77, 331-340.

Gómez, F. y Claustre, H., 2003. The genus *Asterodinium* (Dinophyceae) as a possible biological indicator of warming in the Western Mediterranean Sea. Journal of the *Marine Biological Association of United Kingdom* 83, 173-174.

Gómez, F., Yoshimatsu, S. y Furuya, K., 2005. Morphology of *Brachidinium capitatum* F.J.R. Taylor (Brachidiniales, Dinophyceae) collected from the western Pacific Ocean. *Cryptogamie Algologie* 26, 165-175.

Gómez, F., Nagahama, Y., Takayama, H. y Furuya, K., 2005. Is *Karenia* a synonym of *Asterodinium-Brachidinium*? (Gymnodiniales, Dinophyceae). *Acta Botanica Croatica* 64, 263-274

Gómez, F., 2006. The Dinoflagellate Genera *Brachidinium*, *Asterodinium*, *Microceratium* and *Karenia* in the Open SE Pacific Ocean. *Algae* 21, 445-452.

Gómez, F., 2007. Gómez, F., 2007. Observations on a distinctive H-shaped dinoflagellate. An example of the projection of body extensions in gymnodinioid cells. *Acta Botanica Croatica* 66, aceptado.

4.2.2 *Ceratoperidinium*

Otro dinoflagelado cuyas largas extensiones lo hace muy distintivo es *Ceratoperidinium*. Sin embargo las citas de esta especie han sido escasas. Margalef (1969) describió este género en la costa de Castellón. A pesar de que Margalef no hace referencia a la existencia de placas tecales, Loeblich III (1980) interpreta que un supuesto poro apical justifica la ocurrencia de placas tecales y crea la familia Ceratoperidiniaceae dentro del orden Peridiniales, y además, ilegítimamente propone *Ceratoperidinium margalefii*. Abboud-Abi Saab (1989) encuentra *C. yeye* y otros especimenes con morfología variable y describe uno de ellos con una extensión apical como *Ceratoperidinium mediterraneum*.

En esta memoria se tratan cuestiones como cuántas especies de *Ceratoperidinium* existen y si es un dinoflagelado tecado. Sin embargo, la naturaleza de este dinoflagelado requiere aún más estudios, ya que también podría tratarse del una parte del ciclo de vida de otro dinoflagelado más conocido.

Gómez, F. y Abboud-Abi Saab, M., 2003. Records of *Ceratoperidinium* Margalef (Dinophyceae) from the Mediterranean Sea. *Vie et Milieu* 53, 43-46.

Gómez, F., Nagahama, Y., Fukuyo, Y. y Furuya, K., 2004. Observations on *Ceratoperidinium* (Dinophyceae). *Phycologia* 43, 416-421.

4.2.3 *Gynogonadinium* gen. prov.

Además de los insuficientemente conocidos, *Brachidinium*, *Asterodinium*, *Microceratium* y *Ceratoperidinium* y otros atecados con extensiones, existen otros dinoflagelados nunca descritos. *Gynogonadinium* ha sido estudiado usando microscopía óptica, epifluorescencia e incluso microscopía electrónica de barrido y se propone como nuevo género y nueva especie. La inclusión en esta memoria no constituye una publicación válida del género, actualmente en proceso de revisión, pero permite dejar constancia de su existencia y una información útil para otros investigadores.

Gómez, F. *Gynogonadinium aequatoriale*, gen. et sp. nov. a new dinoflagellate from the open western Equatorial Pacific. *Algae*, enviado.

4.2.4 Noctilucales: *Scaphodinium, Petalodinium, Leptodiscus, Spatulodinium, Kofoidinium, Pomatodinium.*

La especie tipo del orden Noctilucales, *Noctiluca scintillans*, es el primer dinoflagelado conocido y una de las especies de dinoflagelados más estudiada, sin embargo eso contrasta con el escaso conocimiento del resto de las Noctilucales. La poca información existente se basa en los estudios realizados hace tres décadas por J. y M. Cachon. Taylor (2004) remarcaba que la falta de estudios filogenéticos en Noctilucales, ya que actualmente la única secuencia disponible es de *Noctiluca scintillans* y su posición es variable en los árboles filogenéticos. Eso dificulta conocer la posición sistemática de este grupo esencial en la evolución de dinoflagelados. Además, de una familia exclusiva para *Noctiluca*, el orden Noctilucales lo forman las familias kofoidiniaceae y Leptodiscaceae. Las kofoidiniaceas presentan células gymnodiniodes en la mayor parte de su ciclo de vida, dos flagelos y el tipo de núcleo sugieren una proximidad con gymnodiniaceas. Sin embargo, las leptodicaceas carecen del flagelo transversal o esta muy modificado. En esta memoria se muestra una estructura conocida como *ampulla* en el núcleo de *Petalodinium* que sugiere una relación entre *Noctiluca* y las leptodiscaceas. Cachon y Cachon (1969) ilustran un tentativo estado juvenil de *Scaphodinium* con varias filas de cilios, lo que sugiere una relación con entre leptodiscaceas y ciliados. En cualquier caso, las diferencias entre las kofoidiniaceas y las leptodiscaceas son demasiado grandes como para incluirlas en el mismo orden. Sin duda las noctilucaceas son un grupo esencial para comprender la evolución de los dinoflagelados, pero lamentablemente han sido ignorados.

Gómez, F. y Furuya, K., 2004. New records of *Scaphodinium mirabile* (Dinophyceae), an unnoticed dinoflagellate in the Pacific Ocean. *Phycological Research* 52, 13-16.

Gómez, F. y Furuya, K., 2005. *Leptodiscaceans* (Noctilucales, Dinophyceae) from the Pacific Ocean: First records of *Petalodinium* and *Leptodiscus* beyond the Mediterranean Sea. *European Journal of Protistology* 41, 231-239.

Gómez, F. y Furuya, K. 2007, *Kofoidinium*, *Spatulodinium* and other kofoidiniaceans (Noctilucales, Dinophyceae) in the Pacific Ocean. *European Journal of Protistology* 43, aceptado.

Gómez, F. y Souissi, S. On the ecology and unusual life cycle of the dinoflagellate *Spatulodinium pseudonoctiluca* in the NE English Channel. *Comptes Rendus Biologies*, enviado.

4.2.5 Dinophysiales: *Histioneis*

Los Dinophysiales son dinoflagelados tecados que incluyen algunas de las especies más bellamente ornamentadas. El género *Dinophysis*, común en aguas costeras y con algunas especies tóxicas, ha sido objeto de numerosos estudios (Reguera *et al.*, 1995), pero poco se sabe de otros géneros que predominan en aguas abiertas. *Amphisolenia* es relativamente común comparado con *Histioneis* y *Citharistes*. *Triposolenia* es un género muy raro. Basándose en especimenes únicos, un gran número de especies de *Amphisolenia* surgieron basadas en pequeñas diferencias en la forma del cíngulo, de su reducida epiteca y pequeños detalles como las espinas antapicales. A todas luces, si extrapolamos la variabilidad intraespecífica conocida en *Dinophysis* a los otros géneros, podemos considerar que se han debido describir en exceso nuevas especies de Dinophysiales. Todos estos caracteres morfológicos, faltando microscopía electrónica de barrido en este estudio, no han podido ser estudiados y por tanto una revisión de *Amphisolenia* y *Triposolenia* tendrá que esperar. El caso de *Histioneis*, de mayor tamaño y con una desarrollada aleta sulcal, es utilizado en esta memoria para ilustrar las dudas en la validez de muchas de las especies descritas.

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5. Conclusiones

1. Los dinoflagelados marinos libres conocidos quedan agrupados en unas 1555 especies. La variabilidad intraespecífica durante el ciclo de vida o las adaptaciones morfológicas a las condiciones ambientales no han sido tenidas en cuenta por lo que se han descrito un excesivo número de especies.
2. La mayor parte de las especies de dinoflagelados planctónicos tienen una distribución cosmopolita y son escasos los ejemplos de especies restringidas a una región oceánica. La falta de estudios que cubran vastas regiones oceánicas es responsable del aparente endemismo de algunas especies.
3. Se han citado unas 673 especies en el Mar Mediterráneo, en su mayoría en el Mar de Liguria y 267 especies en el Mar Negro. Las escasas especies que resultan endémicas o de origen Indo-Pacífico son de dudosa validez.
4. Los grupos de dinoflagelados poco conocidos seleccionados para su estudio taxonómico han permitido concluir:
   4.1. El orden Brachidiniales esta compuesto de células gymnodinioides con la capacidad de proyectar extensiones del cuerpo celular en condiciones oceánicas. Las brachidiniaceas se pueden reducir a una o varias especies muy versátiles morfológicamente que en aguas costeras han sido recientemente descritas bajo el género *Karenia*. En aguas oceánicas, las formas *Asterodinium* y *Microceratium* predominan en aguas profundas cerca del límite de la zona fótica y *Brachidinium* cerca de la superficie. Las formas afines a *Karenia papilionacea* predominan en aguas neríticas. Otra especie atecada con forma de "H" debido a la proyección de unas distintivas extensiones ha sido ilustrada.
   4.2. *Ceratoperidinium*, encontrada por primera vez en el Pacífico, no presenta placas tecales al menos en la forma *Ceratoperidinium* de su ciclo de vida. *Ceratoperidinium yeye* y *C. mediterraneum* son sinónimas y tan sólo corresponden a un grado diferente del desarrollo de la extensión apical.
   4.3. El nuevo género *Gynogonadinium* se propone sobre la base de su distintiva morfología, designando la especie tipo *G. aequatoriale*. Este nuevo género es un ejemplo del desconocimiento de la diversidad de dinoflagelados atecados en aguas oceánicas tropicales.
   4.4. Las kofoidiniaceas y leptodiscaceas se han agrupado en el orden Noctilucales a pesar de su escasa relación taxonómica. Las kofoidiniaceas

corresponden a células gymnodinioides que se aplanan extraordinariamente en su estadio adulto. En el caso de las leptodiscaceas su ciclo de vida es desconocido y la ausencia de observaciones parece estar ligada a su morfología altamente modificada para el patrón normal de los dinoflagelados. La presencia de *ampulla* en el prominente núcleo de las leptodiscaceas es un carácter común con *Noctiluca*, lo que podría servir para confirmar la relación filogenética entre leptodiscaceas y *Noctiluca.* Sobre la base de la divergente morfología de las leptodiscaceas, su consideración como dinoflagelados necesita ser investigada.

4.4.1. *Scaphodinium mirabile* a pesar de ser común en aguas templadas y tropicales del Pacífico, no había sido previamente citada. Los géneros *Leptodiscus* y *Petalodinium* se citan por primera vez fuera del Mediterráneo y dan muestra de la considerable diversidad de leptodiscaceas, que debido a su fragilidad, transparencia y morfología altamente modificada han pasado desapercibidas. Existen géneros de leptodiscaceas, ilustradas en la presente memoria, aún por describir en aguas oceánicas.

4.4.2. Entre las kofoidiniaceas, el género *Kofoidinium* es el más común en aguas templadas y tropicales. En la localidad tipo, el Canal de la Mancha, se han identificado estadios inmaduros de *Spatulodinium pseudonoctiluca* que habían sido previamente considerados como especies diferentes. *Spatulodinium* era un género monotípico exclusivamente conocido en aguas boreales. Por primera vez se ha encontrado en aguas tropicales y en el hemisferio austral. Además de la especie tipo, especimenes con cloroplastos se encontraron en aguas tropicales, siendo el primer ejemplo de una especie autótrofa en Noctilucales. Además del género *Pomatodinium*, otras kofoidiniaceas, incluyendo especies con microalgas simbiontes, han sido ilustradas.

4.5. Las Dinophysiales presentan modificaciones de la aleta sulcal dependiendo de las condiciones ambientales o estadios de desarrollo, lo que no justifica la consideración de especies diferentes. El género *Histioneis* se ha utilizado como ejemplo para ilustrar la descripción excesiva de especies sobre la base de características cuyos parámetros de variabilidad eran desconocidos.

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